Impacts du changement global sur les cycles biogéochimiques de l'eau et des nutriments dans le système sol–plante et conséquences pour la croissance de la végétation en Sibérie du sud-ouest

Felix Bredoire

université de BORDEAUX

THÈSE PRÉSENTÉE
POUR OBTENIR LE GRADE DE

DOCTEUR DE
L'UNIVERSITÉ DE BORDEAUX

ÉCOLE DOCTORALE SCIENCES ET ENVIRONNEMENTS
SPÉCIALITÉ ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES COMMUNAUTÉS

Par Félix Brédoire

Impacts du changement global sur les cycles biogéochimiques de l'eau et des nutriments dans le système sol–plante et conséquences pour la croissance de la végétation en Sibérie du sud-ouest

Impacts of Global Change on the Biogeochemical Cycling of Water and Nutrients in the Soil–Plant System and Consequences for Vegetation Growth in South-Western Siberia

Sous la direction de : Mark R. Bakker
Co-encadrement : Delphine Derrien et Bernhard Zeller

Soutenue le 31 mars 2016

Membres du jury :

Mme Alexia Stokes, *Directrice de recherche, INRA, Montpellier* . . . . . Présidente
Mme Friederike Lang, *Professeure, Albert-Ludwigs-Universität, Freiburg* . . . . . Rapportrice
M. Renato Marques, *Professeur, Universidade Federal do Paraná, Curitiba* . . . . . Rapporteur
M. Pavel A. Barsukov, *Leading researcher, Institute of Soil Sciences and Agrochemistry, Novossibirsk* Examinateur
M. Hendrik Davi, *Chargé de recherche, INRA, Avignon* . . . . . Examinateur
M. Mark R. Bakker, *Ingénieur de recherche, Bordeaux Sciences Agro–INRA, Bordeaux* . . . . . Directeur de thèse
Mme Delphine Derrien, *Chargée de recherche, INRA, Nancy* . . . . . Co-encadrante de thèse

Impacts of Global Change on the Biogeochemical Cycling of Water and Nutrients in the Soil–Plant System and Consequences for Vegetation Growth in South-Western Siberia

Félix Brédoire

2016

Université de Bordeaux

Résumé

Dans un contexte de changement global, prédire l'évolution de la productivité de la végétation dans le sud-ouest (SO) Sibérien reste un défi du fait d'incertitudes fortes sur les processus régulant la disponibilité en eau et en nutriments. Nous avons mis en évidence des relations entre cycles biogéochimiques, climat et propriétés du sol sur six sites contrastés.

La croissance radiale des tiges de peuplier est principalement sensible au bilan hydrique du sol en forêt de steppe, au sud du SO Sibérien, alors qu'elle est stimulée par de hautes températures estivales en sub-taïga, dans le nord de la région.

Des mesures de terrain et des simulations du bilan hydrique du sol ont montré que la fonte des neiges est importante pour la recharge des réserves hydriques du sol au sud. Au nord, ces réserves sont souvent rechargées en automne. La fonte des neiges est alors associée à du drainage. De plus, au nord, une épaisse couverture de neige protège le sol du gel en hiver. La distribution des racines fines est plus profonde en forêt de steppe qu'en sub-taïga, impactée par le déficit hydrique et le gel.

L'homogénéité du statut en phosphore (P) des sols dans le SO Sibérien montre qu'il n'est pas encore très impacté par la pédogénèse. Les stocks en P élevés, notamment les formes disponibles pour les plantes, suggèrent que le P n'est pas et ne sera pas limitant dans le futur.

La décomposition des litières aériennes et la libération de l'azote (N) sont plus rapides en sub-taïga qu'en forêt de steppe. Un fort drainage pourrait expliquer un transfert profond du N dans les sols en sub-taïga. Cependant ces sols semblent efficaces pour retenir le N, limitant les pertes pour le système sol–plante.

Mots-Clés : Sibérie du sud-ouest, changement global, neige, température du sol, bilan hydrique du sol, cerne, phosphore, azote, racines fines, isotopes, peuplier, prairie

Abstract

Predicting the evolution of vegetation productivity in SW Siberia in the context of global change remains a challenge because of major uncertainties concerning the biogeochemical cycling and the plant-availability of water and nutrients. We provided insights on their relation to climate and soil properties, investigating six contrasting sites.

Aspen stem radial growth is mainly sensitive to soil water budget in the forest-steppe zone established in the south of SW Siberia while it is enhanced by high summer temperatures in the sub-taiga, in the north of the region.

Field measurements and water budget simulations revealed that snow-melt is important re-filling soil water reserves in the south. In the north, these reserves are mostly re-filled in autumn and snow-melt is associated with drainage. A thick snow-pack also prevents soil from freezing in winter in the sub-taiga. Water deficit and soil freezing largely impact the distribution of fine roots within the soil profile which is deeper in forest-steppe than in sub-taiga.

The homogeneous soil phosphorus (P) status in the region investigated revealed this nutrient has not been yet very impacted by contrasting soil processes. High P stocks, and in particular plant-available forms, suggest P is unlikely to be limiting under current and future conditions.

By contrast, we found differences in nitrogen (N) status. Above-ground litter decay and the release of N occurs faster in sub-taiga than in forest-steppe. Higher drainage may explain deeper N transfer in sub-taiga soils. However, sub-taiga soils also seem to be efficient in retaining N, limiting losses from the soil–plant system.

Keywords south-western Siberia, global change, snow, soil temperature, soil water budget, tree-ring, phosphorus, nitrogen, fine roots, isotopes, aspen, grassland

Résumé substantiel

1 Contexte

1.1 Sibérie et changement climatique

Caractéristiques générales de la Sibérie

La Sibérie couvre environ 10 millions de km^2 dans le nord de l'Eurasie, soit 7 % des terres émergées (Groisman et al. 2012a). Elle s'étend de 45 à 75 °N de latitude, et couvre une grande diversité de conditions naturelles, climats, sols, écosystèmes et paysages (Shvidenko et al. 2012). De ce fait, la Sibérie a un poids prépondérant dans la régulation des processus environnementaux à l'échelle globale, notamment sur les cycles biogéochimiques et les rétroactions climatiques (Goetz et al. 2007 ; Groisman et al. 2012a ; McGuire et al. 2007). Le sud-ouest de la Sibérie concentre la plus forte densité de population. Ceci est lié aux conditions climatiques (saison de végétation plus longue et plus chaude que dans le reste de la Sibérie) ainsi qu'à la présence, dans une vaste plaine, de sols de type Chernozem, réputés favorables à l'agriculture.

Le changement climatique en Sibérie

La Sibérie subit un changement climatique rapide et intense (IPCC 2013). Au siècle dernier, la température annuelle moyenne de l'air a augmenté d'environ 1.39 °C en Sibérie, ce qui est plus élevé que sur l'Eurasie du Nord (1.29 °C), l'Arctique (1.28 °C), ou l'ensemble de l'hémisphère nord (0.77 °C) (Groisman et al. 2012b). Une augmentation des précipitations hivernales a également été observée sur la majeure partie de la Sibérie (IPCC 2013). Ainsi, l'épaisseur maximale de neige, le nombre de jours avec plus de 20 cm de neige, et l'équivalent en eau de la neige ont augmenté au cours des dernières décennies (Bulygina et al. 2011, 2010, 2009).

Les projections climatiques indiquent une poursuite de l'augmentation des températures atmosphériques (+2 à +9 °C entre décembre et février et +2 à +6.5 °C entre juin et août pour la fin du XXI^e siècle par rapport à la moyenne de 1986–2005 ; IPCC 2013). Les précipitations devraient également augmenter, mais il y a une plus grande incertitude dans les projections. Les précipitations hivernales devraient être plus fréquentes et plus intenses, ce qui augmenterait notamment l'épaisseur de la couverture neigeuse. En été, les précipitations diminueraient légèrement.

Les modèles bioclimatiques prédisent, d'ici la fin du XXI^{e} siècle, concomitamment à la redistribution et au changement de composition des communautés végétales (Jiang et al. 2012 ; Kicklighter et al. 2014 ; Lucht et al. 2006 ; Shuman et al. 2015 ; Soja et al. 2007 ; Tchebakova et al. 2009, 2010), une augmentation considérable de la surface cultivable en Sibérie. Notamment, les zones favorables aux cultures traditionnelles (blé, maïs ensilage, avoine, seigle, millet) s'étendraient vers le nord et de nouvelles cultures (comme le maïs grain, la betterave à sucre ou les haricots) pourraient être développées dans certaines zones (Kicklighter et al. 2014 ; Tchebakova et al. 2011). Cependant, ces modèles ne tiennent pas compte de la fertilité des sols — qui résulte notamment des stocks bio-disponibles et de la dynamique de l'eau et des nutriments dans le système sol–plante. Les sols de cette région contiennent d'importants stocks de matières organiques et potentiellement d'importants stocks de nutriments. Toutefois, les niveaux actuel et futur de disponibilité pour les plantes des éléments nutritifs demeurent inconnus.

1.2 Objectifs généraux

L'objectif général du projet était de contribuer à l'évaluation de la fertilité des écosystèmes du sud-ouest de la Sibérie, à la compréhension des mécanismes qui la régissent ainsi qu'à son évolution possible dans le contexte du changement climatique. En particulier, nous nous sommes intéressés à la disponibilité des ressources nécessaires à la croissance de la végétation — eau et nutriments — et à son contrôle par le climat. Nous avons porté une attention particulière au rôle de la quantité de neige sur les régimes hydrique et thermique des sols. Nous avons ensuite étudié comment le pédo-climat affecte la décomposition des matières organiques, et donc la libération des éléments nutritifs contenus dans ces matières organiques, les rendant disponibles au prélèvement par la végétation. Ces résultats ont été mis en regard avec les stocks en éléments nutritifs présents dans les sols et l'exploration du profil de sol par les racines fines — qui sont responsables de la majorité du prélèvement d'eau et de nutriments par la plante. Enfin, l'impact des variations inter-annuelles du climat sur la croissance radiale des tiges de peuplier a été étudié.

2 Démarche

2.1 Sites d'étude

Six sites ont été sélectionnés en Sibérie du sud-ouest. Ils sont positionnés le long d'un gradient bioclimatique, depuis la sub-taïga, dans le nord de la zone d'étude, à la zone de steppe, dans le sud.

Pour la zone d'étude, la température moyenne annuelle varie de +0.8 °C dans la

sub-taïga à +3 °C dans la zone de steppe, avec de larges amplitudes saisonnières (−18 à −14 °C en moyenne l'hiver, avec des extrêmes inférieurs à −40 °C, contre +17 à +20 °C en été, avec des extrêmes supérieurs à +30 °C). Les précipitations annuelles moyennes varient de 570 à 320 mm du nord au sud. Une grande partie des précipitations se produit pendant l'hiver, favorisant le développement d'une couverture neigeuse, qui est plus épaisse au nord. En fonction de son épaisseur, la couverture de neige peut empêcher le sol de geler durant l'hiver — situation habituelle dans la sub-taïga. Aussi, la durée de l'enneigement est plus longue et la longueur de la période de végétation plus courte dans le nord que dans le sud de la zone d'étude. Les forêts ne présentent pas les mêmes caractéristiques le long de ce gradient climatique. De grandes forêts couvrent le nord de la région, tandis que des bosquets, de quelques hectares tout au plus, sont disséminés dans de vastes prairies dans le sud.

Tomsk (TOM), dans le nord de la zone étudiée, et Krasnoserskoye (KRA), dans le sud, correspondent aux extrema du gradient bioclimatique. Chebula (CHE), Salair Ouest (SAW), Barnaul (BAR) et Salair Est (SAE) sont caractérisés par des conditions climatiques intermédiaires. En raison de la topographie, l'air humide venant de l'Ouest se condense sur le versant occidental des montagnes du Salair, qui présente par conséquent des caractéristiques typiques de la sub-taïga. Le versant oriental des montagnes du Salair est beaucoup plus sec et correspond à une transition entre la sub-taïga et la forêt de steppe.

Les sites étudiés sont situés au niveau de la ceinture de lœss eurasienne, une vaste zone allant de 40 à 60 °N de latitude nord. Les sols développés sur ce lœss présentent une texture et une minéralogie favorable à la croissance des plantes. Ils ont toutefois des caractéristiques différentes en raison des conditions climatiques et de la couverture végétale qui diffèrent. À KRA, BAR, CHE et SAE, les principaux processus de pédogenèse sont l'accumulation de matière organique et le lessivage des carbonates ; les sols appartiennent aux groupes des Chernozems et Phaeozems. À SAW et TOM, les sols sont soumis à des mouvements de la nappe phréatique, et sont périodiquement saturés en eau. En conséquence, la lixiviation des carbonates et le lessivage des argiles sont des processus importants de pédogenèse ; les sols appartiennent au groupe des Luvisols.

À l'exception du site forestier de SAW, tous les sites présentent des parcelles sous forêt de peuplier tremble (*Populus tremula* L.) avec canopée fermée, et des parcelles en prairies.

2.2 Méthodes

Approche générale

Afin d'étudier l'impact de l'intensité des précipitations neigeuses sur le pédo-climat et les processus se déroulant dans les sols, nous avons combiné : (i) des observations sur un gradient d'enneigement, incluant six sites qui ont été instrumentés au début du projet en 2012–2013, (ii) une approche dendrochronologique, (iii) une modélisation du régime hydrique des sols et (iv) des manipulations de neige, qui ont été effectuées au cours des hivers 2013–2014 et 2014–2015. Les manipulations de neige ont été effectuées uniquement à BAR et TOM, en raison de la difficulté à accéder aux autres sites pendant l'hiver.

Suivi du pédo-climat

Les sites ont été équipés de sondes de température positionnées à 5, 15, et 60 cm de profondeur dans le sol, et également à 2 m au-dessus de la surface du sol. Des capteurs d'humidité ont été installés à 15 et 60 cm de profondeur à TOM et à BAR.

Détermination des propriétés du sol

Tous les sols ont été décrits sur fosse. Pour chaque site et sous chaque couvert de végétation étudié, nous avons décrit et prélevé le sol sur trois fosses indépendantes. Les principales propriétés du sol (densité, texture, pH, teneurs en nutriments majeurs, cations échangeables, etc.) ont été déterminées sur le premier mètre de profondeur.

Caractérisation des profils de racines fines

Nous avons évalué la longueur et la masse des racines fines (diamètre < 0.8 mm) jusqu'à un mètre sous forêts et prairies. Nous avons catégorisé les racines fines en fonction de leur diamètre. En forêt, nous avons aussi distingué les racines de peuplier de celles de la végétation du sous-bois.

Modélisation du régime hydrique des sols

Le modèle Biljou (Granier et al. 1999) a été utilisé afin de simuler les flux d'eau dans les sols et d'identifier les événements de sécheresse. Le modèle calcule la teneur en eau du sol, à un pas de temps journalier, en fonction des précipitations totales, de l'interception des précipitations, de l'évapo-transpiration du couvert végétal et du drainage dans le sol. Il a été étalonné à TOM et BAR, où des sondes d'humidité ont été installées. Le modèle a ensuite été utilisé afin de prédire le régime hydrique des sols en testant divers scénarios de changement climatique (conditions plus sèches en été, niveaux variables de neige).

Dendrochronologie

Sur chacun des six sites, 15 arbres dominants ont été carottés, à une hauteur de 1.30 m, avec une tarière de Pressler de diamètre 5 mm. Les largeurs des cernes ont été mesurées et datées. Nous avons exploré les relations entre la largeur des cernes et divers index climatiques générés à partir de l'analyse des archives météorologiques russes.

Stocks et dynamiques des nutriments

Les stocks et dynamiques de l'azote (N) et du phosphore (P) ont été étudiés en combinant des approches classiques avec des techniques isotopiques. La disponibilité de P a été évaluée par cinétique de dilution isotopique (Fardeau 1996 ; Frossard et Sinaj 1997 ; Frossard et al. 2011). La libération de N par la litière en décomposition, son incorporation dans le profil de sol et son absorption par la végétation ont été évaluées en appliquant in situ des litières marquées au ^{15}N (Zeller et al. 2001). Le devenir du traceur ^{15}N dans l'écosystème a ensuite été suivi durant trois ans.

3 Résultats

3.1 Régimes thermique et hydrique des sols

Nous nous sommes intéressés aux questions suivantes : (1) Quels sont actuellement les régimes de température et d'humidité dans les sols de la forêt de steppe et de la sub-taïga ? (2) Comment les variations climatiques, et en particulier de la quantité de neige, influencent la température et l'humidité du sol dans ces situations pédo-climatiques contrastées ? Nous avons focalisé nos travaux sur les sites de BAR et TOM, localisés respectivement en forêt de steppe et en sub-taïga.

Caractéristiques enregistrées sur la période 1981–2010 : À TOM et à BAR, lorsque le sol n'est pas couvert par la neige, la température du sol est étroitement liée à la température de l'air. Habituellement, à TOM, la couverture de neige est élevée (71 cm, en moyenne, au climax) et le sol ne gèle pas en hiver. À BAR, la couverture de neige est plus faible (49 cm au climax) et le sol gèle pendant l'hiver. En été, la température du sol est généralement plus élevée à BAR qu'à TOM.

Expérience de manipulation de neige : La première manipulation de la neige a été réalisée en 2013–2014, au cours d'un hiver atypique — les chutes de neige ont eu lieu très tard dans la saison et en faible quantité. La seconde manipulation de neige a eu lieu en 2014–2015 — une année marquée par des chutes de neige très abondantes. Les manipulations de neige ont en moyenne permis d'augmenter l'épaisseur de

neige de 25 à 50 cm (+30–100 % de l'épaisseur de neige en conditions naturelles), sur une superficie de 500 m^2.

À BAR, site en forêt de steppe, la manipulation de neige a empêché le sol de geler en forêt. En prairie, le sol a gelé malgré l'ajout de neige, probablement en raison du vent balayant la neige apportée. À la période de la fonte des neiges, pour les deux hivers étudiés, l'humidité et la température du sol ont augmenté 5 à 10 jours plus tard dans le traitement avec ajout de neige par rapport au contrôle. L'humidité du sol à la fonte des neiges était plus élevée dans le traitement avec ajout de neige que dans le contrôle.

À TOM, site en sub-taïga, durant toute la période de suivi du pédo-climat, la température du sol est toujours restée positive. À la fonte des neiges, l'élévation de la température du sol a eu lieu 10–15 jours plus tôt sous le contrôle que sous le traitement neige. En revanche, le sol a été saturé en eau dans les deux cas.

Modélisation du régime hydrique des sols : La calibration du modèle Biljou pour les sites de TOM et BAR a d'abord été réalisée sur la période 2013–2015, période pour laquelle nous disposions de données de terrain mesurées. Puis, en utilisant les paramètres calibrés et les archives météorologiques, nous avons reconstitué le régime hydrique du sol au cours des 46 dernières années. Cette modélisation a montré que la teneur en humidité du sol est au plus faible durant la période estivale sur les deux sites d'étude. À BAR, on observe souvent des déficits en eau et la fonte des neiges, au printemps, est importante pour recharger la réserve en eau du sol. À TOM, les précipitations d'automne permettent généralement une recharge complète de la réserve en eau et le sol et ce dernier est rapidement saturé lors de la fonte des neiges. Nos simulations indiquent alors un plus fort drainage qu'à BAR (les observations de terrain suggèrent qu'il y a peut-être aussi du ruissellement de surface).

Nous avons également effectué des simulations de l'évolution possible du régime hydrique du sol sous différents scénarios climatiques (température plus élevée, été plus sec et diverses intensités de précipitations hivernales). À BAR, des déficits hydriques annuels longs et intenses sont susceptibles de devenir la situation habituelle. La période de stress hydrique arriverait plus tôt, serait de plus longue durée et d'intensité plus élevée qu'actuellement. La teneur en eau du sol à BAR deviendrait fortement dépendante de la quantité de neige tombée en hiver et de l'intensité du déficit hydrique lors de la saison de végétation précédente. À TOM, des déficits hydriques pourraient se produire certaines années dans le futur. Cependant, le stress hydrique pourrait y être modulé par les propriétés du sol qui est assez argileux. Dans les deux cas, une saison de végétation plus précoce augmenterait le prélèvement d'eau au sein du profil du sol.

Dans les deux sites, si les niveaux de neige diminuent, le drainage diminuerait

sensiblement. Si elles augmentent de 50 %, le drainage n'augmenterait que peu. Quel que soit le scénario, l'essentiel du drainage annuel aura lieu à la fonte des neiges. Cette question du drainage nécessite des investigations complémentaires. Notamment, il nous apparaît important dans l'avenir de quantifier ce drainage et de mesurer les concentrations en nutriments exportés dans l'eau de drainage, afin d'appréhender les éventuelles pertes de fertilité induites par la fonte de la neige.

3.2 Dendrochronologie : contrôle climatique de la croissance radiale du peuplier le long d'un gradient de conditions pédo-climatiques

En complément de nos résultats sur le régime hydrique du sol sur deux sites représentatifs de la sub-taïga et de la forêt de steppe, nous avons étudié les archives dendrochronologiques sur l'ensemble de nos sites d'étude. L'enjeu était : (1) d'identifier les déterminants climatiques sur la croissance des arbres dans la zone d'étude et, en particulier, (2) d'évaluer l'influence de la neige sur la croissance des arbres.

Nos résultats révèlent que la croissance radiale de *Populus tremula* L. répond aux variables climatiques de façon contrastée entre les sites situés dans le sud de la zone d'étude (steppe et sud de la forêt de steppe), et ceux situés plus au nord (nord de la forêt de steppe, sub-taïga).

Dans le sud de notre région d'étude, qui connaît des conditions climatiques plus sèches que dans le nord, la croissance radiale est surtout sensible au régime hydrique du sol en été. Elle augmente quand les précipitations estivales augmentent. Elle diminue avec l'élévation des températures de l'air et du sol, et quand l'arbre est soumis à un stress hydrique. Le régime hydrique du sol peut aussi avoir des répercussions sur la croissance de l'année suivante. Enfin, des températures élevées se produisant tôt et tard dans la saison de végétation ont tendance à améliorer la croissance des arbres.

Dans le nord de la forêt-steppe et dans la sub-taïga, la croissance radiale de *Populus tremula* L. est essentiellement stimulée par des températures de l'air et du sol élevées durant l'été. Une explication possible est que ces températures estivales élevées augmentent l'activité microbienne, la minéralisation de la matière organique, donc la libération d'éléments nutritifs, ainsi que le débit massique et la diffusion des sèves. En revanche, les températures élevées de l'air et du sol au début du printemps ont un impact négatif sur la croissance des arbres. Une explication possible serait une désynchronisation entre la période de forte disponibilité en éléments nutritifs et la période d'absorption par les plantes.

Nos résultats indiquent, en outre, que les niveaux de croissance radiale moyenne pour un âge donné ont tendance à être plus élevés dans la zone de forêt de steppe que dans la zone de sub-taïga, peut-être en raison des conditions climatiques (température

plus élevée, durée plus longue de la saison de végétation) et/ou des propriétés du sol.

Enfin, nous avons noté une augmentation de la croissance radiale moyenne des dans les dernières décennies. Parmi les explications possibles, encore à investiguer, on peut citer : des températures plus chaudes, une saison de végétation plus longue, la hausse des niveaux de CO_2 dans l'atmosphère ou encore une plus grande disponibilité des éléments nutritifs, en raison de l'augmentation des dépôts atmosphériques (N) ou de la stimulation des processus de décomposition.

3.3 Stocks et dynamiques du N et du P dans le système sol–plante

La disponibilité des éléments nutritifs est un régulateur clé de la productivité primaire et de l'équilibre du carbone des écosystèmes (Chapin et al. 2011 ; Fernández-Martínez et al. 2014 ; Wieder et al. 2015). La disponibilité des nutriments varie à la fois dans l'espace et dans le temps, et cette variabilité peut finalement être plus importante pour la croissance de la végétation que leurs changements physiologiques entraînés par le climat (Lukac et al. 2010). Individuellement ou en combinaison, l'azote (N) et de phosphore (P) sont les principaux éléments nutritifs contraignant les processus biologiques et la productivité primaire (Elser et al. 2007 ; Fay et al. 2015 ; Güsewell 2004 ; Harpole et al. 2011 ; LeBauer et Treseder 2008 ; Vitousek et al. 2010). La section ci-dessous dresse un état de la disponibilité en N et P sur les sites du projet, évaluée en faisant appel à des techniques isotopiques.

Disponibilité du P

Nous avons mesuré des concentrations, des stocks, et une structuration des réservoirs de phosphore (P) relativement homogènes sur l'ensemble de nos sites. L'âge récent des dépôts de lœss, couplé à une lente cinétique de pédogenèse, n'a probablement pas encore mené à un éventail suffisamment large de conditions physico-chimiques induisant différents niveaux de P.

Nous avons toutefois pu noter quelques écarts à cette relative homogénéité qui peuvent être expliqués par les propriétés des sols. Ainsi, à TOM, les battements périodiques de la nappe, responsables de l'accumulation relativement plus forte des argiles et des oxydes dans les couches profondes du sol, contribuent vraisemblablement à expliquer les valeurs élevées de concentrations en P et en ions phosphate diffusifs (en particulier à −60 cm dans les prairies). À KRA, l'accumulation de $CaCO_3$ pourrait être responsable des niveaux élevés d'ions phosphate diffusifs à −100 cm dans les prairies (Hinsinger 2001 ; Kuo et Lotse 1972). À SAE, le matériau de schiste sous-jacent au dépôt de lœss repéré à 80 cm de profondeur est probablement

responsable des basses concentrations en P et des proportions extrêmement faibles d'ions phosphate diffusifs dans les couches profondes.

Nous avons comparé les niveaux de P à la surface (0–20 cm) des sols du sud-ouest de la Sibérie à ceux mesurés dans des contextes de végétation similaires à l'échelle mondiale. Cette comparaison a révélé des niveaux de P total, de P organique et inorganique très élevés dans les horizons de surface des sols du sud-ouest de la Sibérie, mais une quantité de P disponible (estimée par les ions P diffusibles) intermédiaire à l'échelle mondiale. Cependant, les stocks d'ions phosphate disponibles sont importants dans les couches profondes du sol, où l'exploration des racines fines est actuellement faible. Ces résultats suggèrent qu'il est peu probable que le P soit limitant pour la croissance de la végétation et pour le développement de l'agriculture dans les conditions actuelles et dans un avenir proche.

Devenir du N libéré par les litières de feuilles en décomposition

Les litières végétales étant la principale source de N pour le sol, nous avons étudié le devenir du N libéré lors de la décomposition de litières, sur quatre des sites d'étude (TOM, SAW, SAE, BAR), en utilisant des litières de feuilles marquées au ^{15}N.

La décomposition des litières et la libération du N qu'elles contiennent sont plus rapides dans les sites de sub-taïga (TOM et SAW) que dans les sites de forêt de steppe (BAR et SAE). L'incorporation du N dérivé des litières dans le profil de sol est également plus profonde dans les sites de sub-taïga, peut-être en raison du fort enneigement y occasionnant un drainage plus intense qu'en forêt de steppe. Il est cependant probable que les exportations de N hors du système, par drainage, soient limitées grâce aux propriétés physico-chimiques du sol dans la zone de sub-taïga étudiée (sol riche en limons et oxydes favorisant la rétention du N) et par la persistance d'une activité microbienne basale pendant l'hiver dans les sols non-gelés.

Nous avons pu mettre en évidence que le N dérivé des litières était transféré plus profondément dans le profil de sol sous forêt que sous prairie. En outre, nous avons pu mesurer un niveau élevé de traceur ^{15}N issu des litières dans la végétation des prairies ($\delta^{15}\mathrm{N} \approx 200$ ‰ lors du prélèvement effectué au printemps, 6 mois après le dépôt des litières — litière initiale déposée en prairie à 3159 ‰). Le niveau de traceur était beaucoup plus faible à la même date dans la végétation de sous-bois des placettes forestières ($\delta^{15}\mathrm{N} \approx 5$ ‰ — litière initiale déposée en forêt à 528 ‰). L'exploration des racines fines, plus dense en prairie qu'en forêt, a peut-être rendu plus efficace l'absorption de N par la végétation des prairies et limité la migration du N dans le profil de sol. Il est également possible que cette végétation prairiale soit active plus tôt que les arbres et les espèces de sous-bois, à la période où le drainage peut être important.

3.4 Influence des conditions pédo-climatiques contrastées sur la distribution des racines fines

La répartition des racines fines à travers le profil de sol est un bon indicateur pour évaluer les contraintes environnementales affectant les plantes dans l'acquisition de leurs ressources (eau et nutriments). Nous avons donc abordé la question suivante : est-ce que les conditions pédo-climatiques contrastées observées sur notre gradient de sites dans le sud-ouest de la Sibérie induisent des distributions de racines fines distinctes ?

L'exploration des racines fines a tendance à être plus profonde en forêt qu'en prairie. Elle est également plus profonde pour les arbres que pour la végétation de sous-bois dans les peuplements forestiers.

Concernant l'impact du pédo-climat, nous avons pu mettre en évidence que l'exploration des racines fines est plus profonde en forêt de steppe qu'en sub-taïga. La longueur totale et la masse des racines y sont également plus élevées. Ceci est observé sous forêt et sous prairie. Deux types de facteurs pourraient expliquer ces grandes tendances : l'exploration des ressources et les contraintes physiques de l'environnement. Nos recherches sur les dynamiques du P et du N ont révélé que ces nutriments ne sont pas limitants pour la végétation dans les horizons de surface. En revanche, dans la steppe–forêt de steppe, des systèmes racinaires profonds peuvent refléter une stratégie d'acquisition de l'eau car la dessiccation du sol est généralement importante en été, comme discuté précédemment. Dans la sub-taïga, la régulière saturation en eau du profil du sol peut, en revanche, constituer une contrainte physique pour le développement de racines profondes. D'autres contraintes environnementales ont été détectés à l'échelle locale, comme la présence du substratum rocheux à faible profondeur à SAE, sans que ces facteurs ne semblent limitants pour la production primaire dans nos sites d'étude. En outre, le gel du sol induit par la faible couverture neigeuse dans la steppe–forêt de steppe pourrait également favoriser le développement profond des racines fines, en raison d'une mortalité des racines accrue à la surface en hiver. Pour autant que nous le sachions, l'effet du gel sur le profil racinaire n'a encore jamais été étudié et nécessiterait des investigations plus poussées. Il est possible, finalement, que le gel du sol ne nuise pas à la présence de racines fines en surface, et qu'il n'induise qu'un renouvellement des racines plus fréquent (par exemple, chaque hiver).

Les diverses espèces végétales ont des traits différents, parmi lesquels différentes biochimie et décomposabilité des racines, qui impactent les interactions plante–sol et les cycles biogéochimiques (Bardgett et al. 2014 ; Freschet et al. 2012 ; Guo et al. 2008 ; Kong et al. 2014 ; Prieto et al. 2016 ; Roumet et al. 2016, 2006 ; Smith et al. 2014). Ainsi, les racines des espèces de grandes cultures sont plus facilement dégradées que les racines des écosystèmes forestiers. Cette différence de biodégradabilité pourrait être responsable d'une baisse du stock de carbone du sol

lors de la mise en culture de sols forestiers (Prieto et al. 2016) comme cela pourrait être le cas dans le futur dans le sud-ouest de la Sibérie.

Il nous apparaît important d'évaluer la dynamique de renouvellement des racines fines dans le sud-ouest de la Sibérie, car elle est contrôlée par des facteurs variant avec le changement global (Brunner et Godbold 2007 ; Finér et al. 2011 ; Gill et Jackson 2000 ; McCormack et al. 2013 ; McCormack et Guo 2014) et impacte fortement les cycles biogéochimiques du carbone et des nutriments (Clemmensen et al. 2013 ; Ruess et al. 2003 ; Yuan et Chen 2010 ; Yuan et al. 2011).

Enfin, les racines ne sont pas actives de la même façon dans tout le profil de sol. Il serait intéressant de connaître la profondeur de l'absorption racinaire, la variabilité de cette profondeur au cours des saisons, et si différentes espèces ont différentes stratégies pour l'absorption de leurs ressources dans le sud-ouest de la Sibérie. Afin d'appréhender ces questions, des analyses des isotopes de l'eau contenue dans le sol, dans les racines et les feuilles sont en cours sur nos sites d'étude.

4 Synthèse : fonctionnement intégré des cycles biogéochimiques dans les écosystèmes de Sibérie du sud-ouest et prospective dans le contexte du changement climatique

Nos travaux ont mis en évidence que des processus biogéochimiques contrastés opèrent actuellement dans les sols des zones bioclimatiques de forêt de steppe et de sub-taïga dans le sud-ouest de la Sibérie.

Dans la zone de forêt de steppe, le sol gèle en hiver en raison d'une couverture neigeuse peu épaisse. La fonte de la neige constitue la recharge principale d'eau dans le sol. L'été est chaud et sec, ce qui conduit souvent à des déficits en eau dans les horizons de surface, et à une exploration racinaire profonde. La libération du N et du P organiques, qui dépend de la dégradation des matières organiques, est ralentie durant l'hiver et l'été. Les conditions pédo-climatiques difficiles nuisent en effet à l'activité des décomposeurs. Pour cette raison, les terres cultivées sont actuellement souvent fertilisées en N.

Dans la zone de sub-taïga, l'épais manteau neigeux en hiver empêche le sol de geler. La fonte des neiges induit généralement un drainage, car les réserves en eau du sol sont presque rechargées suite aux précipitations automnales. Il n'y a pas de sécheresse en été. Ainsi, la croissance des plantes, et le développement de l'agriculture, sont principalement limités par la courte durée de la saison de végétation et les températures estivales peu élevées. Comme l'eau reste disponible dans les horizons de sol superficiels pendant l'été — et est en excès dans les couches

profondes — les racines fines se concentrent dans les horizons supérieurs du sol. Les conditions pédo-climatiques permettent une dégradation rapide des litières et une incorporation rapide des résidus de ces litières dans les couches supérieures du sol minéral. Le drainage provoqué par la fonte des neiges peut conduire à une exportation des éléments nutritifs sous des formes solubles. Cependant, les propriétés du sol et la persistance d'une activité microbienne basale pendant l'hiver semblent efficacement contrer cet effet et immobiliser le N dérivé des litières dans les horizons supérieurs du profil de sol.

Les projections climatiques indiquent un réchauffement des températures de l'air et des variations de la saisonnalité des précipitations. Entre autres, les précipitations hivernales ont tendance à augmenter. Dans ce contexte, nos travaux indiquent que les processus biogéochimiques opérant dans les sols pourraient évoluer.

Dans la zone de forêt de steppe, les pénuries d'eau dans le sol deviendraient plus fréquentes, plus intenses et plus longues, conduisant probablement à un approfondissement de la distribution des racines fines. Les précipitations hivernales deviendraient cruciales pour la recharge en eau du sol. Les nouveaux régimes de température et d'humidité du sol ralentiront probablement la vitesse de dégradation des matières organiques et, en conséquence, la libération des nutriments contenus dans ces matières organiques. Une incertitude majeure concerne le gel du sol en hiver. Si un manteau neigeux épais apparaît au début de l'hiver, sur un sol non gelé, il devrait être favorable au maintien de l'activité microbienne et à la libération d'éléments nutritifs. Dans un tel cas, le grand stock de nutriments disponibles devrait permettre le développement d'une agriculture durable, sans engrais ou avec une utilisation limitée. Toutefois, les pratiques d'irrigation seront certainement nécessaires pour garantir les rendements des cultures.

Dans la zone de sub-taïga, des pénuries d'eau pourraient apparaître de temps à autre en été. L'augmentation des précipitations hivernales risque d'augmenter le flux de drainage, sauf si la réserve en eau du sol a été épuisée durant la saison de végétation précédente. Dans ce cas précis, la fonte des neiges rechargerait les horizons déficitaires en eau. Il est possible que les racines fines se développent plus profondément pour atteindre l'eau. Il est probable que l'élévation de la température du sol et la disponibilité en eau suffisante stimuleront l'activité microbienne, la dégradation des matières organiques et la libération de leurs éléments nutritifs. Ces effets combinés pourraient entraîner une plus grande productivité et favoriser le développement d'une agriculture durable et sans irrigation.

Références

Bardgett, R. D., Mommer, L. et Vries, F. T. D. (2014). Going underground : root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution* 29.12, 692–699. doi : 10.1016/j.tree.2014.10.006.

Brunner, I. et Godbold, D. L. (2007). Tree roots in a changing world. *Journal of Forest Research* 12 (2), 78–82. doi : 10.1007/s10310-006-0261-4.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N. et Korshunova, N. N. (2011). Changes in snow cover characteristics over Northern Eurasia since 1966. *Environmental Research Letters* 6.4, 045204. doi : 10.1088/1748-9326/6/4/045204.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N. et Radionov, V. F. (2010). Snow cover basal ice layer changes over Northern Eurasia since 1966. *Environmental Research Letters* 5.1, 015004. doi : 10.1088/1748-9326/5/1/015004.

Bulygina, O. N., Razuvaev, V. N. et Korshunova, N. N. (2009). Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters* 4.4, 045026. doi : 10.1088/1748-9326/4/4/045026.

Chapin, F. S., Matson, P. A. et Vitousek, P. M. (2011). *Principles of Terrestrial Ecosystem Ecology (Second Edition)*. Springer Science + Business Media. doi : 10.1007/978-1-4419-9504-9.

Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A. et Lindahl, B. D. (2013). Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. *Science* 339.6127, 1615–1618. doi : 10.1126/science.1231923.

Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B. et Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10.12, 1135–1142. doi : 10.1111/j.1461-0248.2007.01113.x.

Fardeau, J. (1996). Dynamics of phosphate in soils. An isotopic outlook. *Fertilizer Research* 45.2, 91–100. doi : 10.1007/bf00790658.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., Collins, S. L., Davies, K. F., Du, G., Feng, X., Firn, J., Gruner, D. S., Hagenah, N., Hautier, Y., Heckman, R. W., Jin, V. L., Kirkman, K. P., Klein, J., Ladwig, L. M., Li, Q., McCulley, R. L., Melbourne, B. A., Mitchell, C. E., Moore, J. L., Morgan, J. W., Risch, A. C., Schütz, M., Stevens, C. J., Wedin, D. A. et Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants* 1.7, 15080. doi : 10.1038/nplants.2015.80.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., III, F. S. C., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F. et Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4.6, 471–476. doi : 10.1038/nclimate2177.

Finér, L., Ohashi, M., Noguchi, K. et Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* 262.11, 2008–2023. doi : 10.1016/j.foreco.2011.08.042.

Freschet, G. T., Aerts, R. et Cornelissen, J. H. C. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology* 26.1, 56–65. doi : 10.1111/j.1365-2435.2011.01913.x.

Frossard, E. et Sinaj, S. (1997). The isotope exchange kinetic technique : A method to describe the availability of inorganic nutrients. Applications to K, P, S and Zn. *Isotopes in Environmental and Health Studies* 33.1-2, 61–77. doi : 10.1080/10256019808036360.

Frossard, E., Achat, D. L., Bernasconi, S. M., Bünemann, E. K., Fardeau, J.-C., Jansa, J., Morel, C., Rabeharisoa, L., Randriamanantsoa, L., Sinaj, S., Tamburini, F. et Oberson, A. (2011). The use of tracers to investigate phosphate cycling in soil–plant systems. In : *Phosphorus in Action*. T. 100, 59–91. doi : 10.1007/978-3-642-15271-9_3.

Gill, R. A. et Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147.1, 13–31. doi : 10.1046/j.1469-8137.2000.00681.x.

Goetz, S. J., Mack, M. C., Gurney, K. R., Randerson, J. T. et Houghton, R. A. (2007). Ecosystem responses to recent climate change and fire disturbance at northern high latitudes : observations and model results contrasting northern Eurasia and North America. *Environmental Research Letters* 2.4, 045031. doi : 10.1088/1748-9326/2/4/045031.

Granier, A., Bréda, N., Biron, P. et Villette, S. (1999). A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* 116.2–3, 269–283. doi : 10.1016/S0304-3800(98)00205-1.

Groisman, P. Y., Gutman, G., Shvidenko, A. Z., Bergen, K. M., Baklanov, A. A. et Stackhouse Jr, P. W. (2012a). Intoduction : regional features of Siberia. In : *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 1, 1–17. doi : 10.1007/978-94-007-4569-8_1.

Groisman, P. Y., Blyakharchuk, T. A., Chernokulsky, A. V., Arzhanov, M. M., Marchesini, L. B., Bogdanova, E. G., Borzenkova, I. I., Bulygina, O. N., Karpenko, A. A., Karpenko, L. V., Knight, R. W., Khon, V. C., Korovin, G. N., Meshcherskaya, A. V., Mokhov, I. I., Parfenova, E. I., Razuvaev, V. N., Speranskaya, N. A., Tchebakova, N. M. et Vygodskaya, N. N. (2012b). Climate changes in Siberia. In : *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 3, 57–109. doi : 10.1007/978-94-007-4569-8_3.

Guo, D., Li, H., Mitchell, R. J., Han, W., Hendricks, J. J., Fahey, T. J. et Hendrick, R. L. (2008). Fine root heterogeneity by branch order : exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* 177.2, 443–456. doi : 10.1111/j.1469-8137.2007.02242.x.

Güsewell, S. (2004). N : P ratios in terrestrial plants : variation and functional significance. *New Phytologist* 164.2, 243–266. doi : 10.1111/j.1469-8137.2004.01192.x.

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B. et Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters* 14.9, 852–862. doi : 10.1111/j.1461-0248.2011.01651.x.

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes : a review. *Plant and Soil* 237.2, 173–195. doi : 10.1023/A:1013351617532.

IPCC (2013). *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Sous la dir. de T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex et P. Midgley. Cambridge Books Online. Cambridge University Press. 1535 p. doi : 10.1017/CBO9781107415324.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D. et Melillo, J. (2012). Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. *Ecology and Evolution* 2.3, 593–614. doi : 10.1002/ece3.85.

Kicklighter, D. W., Cai, Y., Zhuang, Q., Parfenova, E. I., Paltsev, S., Sokolov, A. P., Melillo, J. M., Reilly, J. M., Tchebakova, N. M. et Lu, X. (2014). Potential influence of climate-induced vegetation shifts on future land use and associated land carbon fluxes in Northern Eurasia. *Environmental Research Letters* 9.3, 035004. doi : 10.1088/1748-9326/9/3/035004.

Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H. et Guo, D. (2014). Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* 203.3, 863–872. doi : 10.1111/nph.12842.

Kuo, S. et Lotse, E. G. (1972). Kinetics of phosphate adsorption by calcium carbonate and Ca-kaolinite1. *Soil Science Society of America Journal* 36.5, 725–729. doi : 10.2136/sssaj1972.03615995003600050015x.

LeBauer, D. S. et Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89.2, 371–379. doi : 10.1890/06-2057.1.

Lucht, W., Schaphoff, S., Erbrecht, T., Heyder, U. et Cramer, W. (2006). Terrestrial vegetation redistribution and carbon balance under climate change. *Carbon Balance and Management* 1.1, 6. doi : 10.1186/1750-0680-1-6.

Lukac, M., Calfapietra, C., Lagomarsino, A. et Loreto, F. (2010). Global climate change and tree nutrition : effects of elevated CO_2 and temperature. *Tree Physiology* 30.9, 1209–1220. doi : 10.1093/treephys/tpq040.

McCormack, M. L., Eissenstat, D. M., Prasad, A. M. et Smithwick, E. A. H. (2013). Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biology* 19.6, 1697–1708. doi : 10.1111/gcb.12163.

McCormack, M. L. et Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science* 5. doi : 10.3389/fpls.2014.00205.

McGuire, A. D., Chapin, F. S., Wirth, C., Apps, M., Bhatti, J., Callaghan, T., Christensen, T. R., Clein, J. S., Fukuda, M., Maximov, T., Onuchin, A., Shvidenko, A. et Vaganov, E. (2007). Terrestrial Ecosystems in a Changing World. In : chap. Responses of High Latitude Ecosystems to Global Change : Potential Consequences for the Climate System, 297–310. doi : 10.1007/978-3-540-32730-1_24.

Prieto, I., Stokes, A. et Roumet, C. (2016). Root functional parameters predict fine root decomposability at the community level. *Journal of Ecology*. doi : 10.1111/1365-2745.12537.

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K.-f. et Stokes, A. (2016). Root structure-function relationships in 74 species : evidence of a root economics spectrum related to carbon economy. *New Phytologist*. doi : 10.1111/nph.13828.

Roumet, C., Urcelay, C. et Diaz, S. (2006). Suites of root traits differ between annual and perennial species growing in the field. *New Phytologist* 170.2, 357–368. doi : 10.1111/j.1469-8137.2006.01667.x.

Ruess, R. W., Hendrick, R. L., Burton, A. J., Pregitzer, K. S., Sveinbjornssön, B., Allen, M. F. et Maurer, G. E. (2003). Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs* 73.4, 643–662. doi : 10.1890/02-4032.

Shuman, J. K., Tchebakova, N. M., Parfenova, E. I., Soja, A. J., Shugart, H. H., Ershov, D. et Holcomb, K. (2015). Forest forecasting with vegetation models across Russia. *Canadian Journal of Forest Research* 45.2, 175–184. doi : 10.1139/cjfr-2014-0138.

Shvidenko, A. Z., Gustafson, E., McGuire, A. D., Kharuk, V. I., Schepaschenko, D. G., Shugart, H. H., Tchebakova, N. M., Vygodskaya, N. N., Onuchin, A. A., Hayes, D. J., McCallum, I., Maksyutov, S., Mukhortova, L. V., Soja, A. J., Belelli-Marchesini, L., Kurbatova, J. A., Oltchev, A. V., Parfenova, E. I. et Shuman, J. K. (2012). Terrestrial Ecosystems and Their Change. In : *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 6, 171–249. doi : 10.1007/978-94-007-4569-8_6.

Smith, S. W., Woodin, S. J., Pakeman, R. J., Johnson, D. et Wal, R. van der (2014). Root traits predict decomposition across a landscape-scale grazing experiment. *New Phytologist* 203.3, 851–862. doi : 10.1111/nph.12845.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S. et Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change : Predictions versus current observations. *Global and Planetary Change* 56.3–4, 274–296. doi : 10.1016/j.gloplacha.2006.07.028.

Tchebakova, N. M., Parfenova, E. I., Lysanova, G. I. et Soja, A. J. (2011). Agroclimatic potential across central Siberia in an altered twenty-first century. *Environmental Research Letters* 6.4, 045207. doi : 10.1088/1748-9326/6/4/045207.

Tchebakova, N. M., Parfenova, E. et Soja, A. J. (2009). The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4.4, 045013. doi : 10.1088/1748-9326/4/4/045013.

Tchebakova, N. M., Rehfeldt, G. E. et Parfenova, E. I. (2010). From vegetation zones to climatypes : Effects of climate warming on Siberian ecosystems. In : *Permafrost Ecosystems. Siberian Larch Forests*. Chap. 22, 427–447.

Vitousek, P. M., Porder, S., Houlton, B. Z. et Chadwick, O. A. (2010). Terrestrial phosphorus limitation : mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications* 20.1, 5–15. doi : 10.1890/08-0127.1.

Wieder, W. R., Cleveland, C. C., Lawrence, D. M. et Bonan, G. B. (2015). Effects of model structural uncertainty on carbon cycle projections : biological nitrogen fixation as a case study. *Environmental Research Letters* 10.4, 044016. doi : 10.1088/1748-9326/10/4/044016.

Yuan, Z. Y. et Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age : Literature review and meta-analyses. *Critical Reviews in Plant Sciences* 29.4, 204–221. doi : 10.1080/07352689.2010.483579.

Yuan, Z., Chen, H. Y. et Reich, P. B. (2011). Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. *Nature Communications* 2, 344. doi : 10.1038/ncomms1346.

Zeller, B., Colin-Belgrand, M., Dambrine, E. et Martin, F. (2001). Fate of nitrogen released from 15N-labeled litter in European beech forests. *Tree Physiology* 21.2-3, 153–162. doi : 10.1093/treephys/21.2-3.153.

Remerciements / Acknowledgements

Quelques mots, tout proches de la surface de l'objet bien qu'ils soient les derniers. Je remercie chaleureusement : / I warmly thank :

Mes trois encadrants de thèse, qui se sont toujours montrés disponibles et enthousiastes, qui m'ont aiguillé sans hésiter vers d'autres personnes plus compétentes (lorsque l'on commencait à se diriger hors de leurs domaines de spécialité) et qui m'ont fait confiance tout au long de ce projet, bien souvent à distance. Mark Bakker, un néerlandais à vélo qui relit, commente et corrige n'importe quel document plus vite que son ombre, ne recule ni devant un bon vieux comptage de racines fines, ni devant un dancefloor improvisé en forêt de steppe entre une falaise et une placette expérimentale (et ce n'est qu'une des inombrables anecdotes dont Mark se souvient et peut alimenter à-propos bien des conversations). Delphine Derrien, la chef du projet en toute humilité, toujours ravie d'apprendre de nouvelles choses. Un grand merci pour le gros coup de main dans la dernière ligne droite… et pour la voiture ! Bernd Zeller, l'homme de tous les terrains, qui se rie de tout (et c'est plutôt communicatif) mais aime le travail bien fait (et les Big Bon). Vos approches complémentaires nous ont permis de réagir face à l'inattendu. Et puis, bien que les directions prises aient parfois été un peu hasardeuses (*no roads…*), nous avons finalement donné quelque forme à cette constellation patatoïdale. Ce fut un plaisir de travailler avec vous !

All the other members of the A-West-CC project. Pavel Barsukov was responsible for all the organization in Siberia. His knowledge of the local context, in all domains, from ecology to life in Siberia—I was always surprised by your capacity to find vehicle (even a city bus !), driver and accommodation in a few phone calls a few days, sometimes even a few hours, before to start a field trip—was precious to define all together research questions and to select field sites. Of course, we cannot predict all what can happen, for example the reaping of an experimental grassland, the burning of crop remnants that goes a bit to far in some of our forest plots, or the drowning of moisture data-loggers because of snow-melt. Anyway, it seems we managed to do some things ! It would have been different without Olga Rusalimova. Notably, she was super efficient on the field and took in charge some boring administrative tasks. Also, she took care of me for practical life issues in Novosibirsk. Thanks for the washing machine and so on. Polina Nikitich was the other PhD student on the project, we worked in pairs on many aspects and that was always a pleasure. Thank you Polina and your parents, Alexander and Svetlana, for your help organizing a

holiday trip at the Lake Baikal. I wish you all the best for the end of your PhD (I hope I will come to your defence in Tomsk at cold wintertime). Zachary Kayler, with who we initiated investigations of water dynamics in the soil–plant system using $^{18}O/^{2}H$ isotopic techniques. I am sorry we still did not managed to finish that. Thank you for your invitations to spend a few weeks at ZALF, in Müncheberg. I do not forget Sébastien Fontaine and Olga Vaishlya, with who I had fewer contacts but I appreciated them. I was glad to meet you all and to work with you, that was a great experience !

Même s'ils n'étaient pas officiellement impliqués dans le projet en Sibérie, ils s'y sont investi avec leurs compétences et leur enthousiasme (eux aussi) : David Achat, Laurent Augusto, Jean-Luc Dupouey et Arnaud Legout.

The members (exterior from the project) of my thesis committee : Nathalie Bréda, Andreas Richter and Grégory van der Heijden.

All those who greatly contributed to field work. They were there very regularly : Alexander Bashuk and Anton Litvinov. The summer team in 2013 : Natalia Gaberman, Nicolaï Kolosov, Iulia Petrashova, Helene Rieckh and Alina Stupak. They participated occasionally : Dima, Genia, Vania and Yegor.

Ils ont contribué à la préparation du travail de terrain, à la préparation des échantillons, aux analyses, etc. à ISSA, ISPA, BEF, EEF, PTEF : / They contributed to field work preparation, samples processing, lab analyses, etc. at ISSA, ISPA, BEF, EEF, PTEF : Galina Bougrovskaia, Serge Didier, Nathalie Gallegos, Christine Gehin, Louisette Gelhaye, François Gérémia, Christian Hossann, Marie-Clotilde Maintenant, Joseph Michel, Sylvie Millin and Sylvie Niollet.

All the colleagues, here or elsewhere, who occasionally answer some of my questions, gave me technical advices, etc. : Nicolas Angeli, Claude Bréchet, Anne Gallet-Budynek, Paul Koeniger, Nicolai Laschinskiy, Rodolphe Lauverjon, Sergey Loiko, Christian Morel, Caroline Plain, Jacques Ranger, Laurent Saint-André, and André Schneider

Elles ont fait face avec efficacité et patience à toutes les tâches administratives, parfois arides, relatives à mes nombreuses missions durant ces trois ans : Patricia Braconnier, Karine Hakim, Isabelle Martin, Jacqueline Noël et Corinne Sert.

They hosted us during field missions : the agronomic station and Pavel Litvinsev in Barnaul ; Tomsk State University, the Petrashova family and Vadim Yartsev in Tomsk ; the mother of Pavel Barsukov in Chebula ; and the agrostation in Krasnozersk.

They hosted me in this nomadic period in Bordeaux, Novossibirsk, Nancy, Berlin or Salagosse : Helene, Ira & Ksushia, Nathalie, Nina, Pavel & Olga, Rodolphe & Gwen, Sasha, Séverine, Yaric and my parents.

All the drivers who brought us more or less safely on our field sites and back, I remember great sensations (Mark too) ! I don't remember all your names guys but I can cite Mhitar, Sasha, Viktor, Youri Vassilievitch…

Les autres collègues de couloir, de bureau, de coin café, de cantine, de pétanque… que je n'ai pas encore cité. À Bordeaux : Sylvie Bussière, Mathias Christina, Cécile Coriou, Jean-Yves Cornu, Sandra Debesa, Florian Delerue, Laurence Denaix, Pascal Denoroy, Hugo Fernández-Mena, Maya Gonzalez, Arthur Guignabert, Évelyne Kouassi, Julien Laurette, Haixiao Li, Olaia Liñero, Eric Martin, Elsa Martineau, Alain Mollier, Thomas Nesme, Christophe Nguyen, Benjamin Nowak, Sylvain Pellerin, Fanny Perrier, Loïc Prud'Homme, John Regan, Bruno Ringeval, Valérie Sappin-Didier, Stéphane Thunot, Yoan Viala, David Vidal, Emma Vivien et Bofang Yan. À Nancy : Léa Bedel, Jérémie Bel, Maximilien Beuret, Séverine Bienaimé, Nicolas Bilot, Pascal Bonnaud, Christophe Calvaruso, Carine Cochet, Mélanie Court, Frédéric Darboux, Jérôme Demaison, Karna Hansson, Gil Kirchen, Zhun Mao, Gilles Nourisson, Benoît Pollier, Arnaud Reichard, Philippe Roux, Jade Salleles, Philippe Santenoise, Nathalie Schvester, Marie-Pierre Turpault et (le dernier mais non le moindre) Jean-Christophe Viennet.

Ainsi que ma famille et mes amis… Ils se reconnaîtront peut-être.

Finally, I thank the members of the jury of my PhD thesis, who positively appreciated the work I presented, our team (see the list above) work : Hendrik Davi, Friederike Lang, Renato Marques and Alexia Stokes.

Exercice périlleux que celui de la liste, vous aurai-je oublié ?

The A-West-CC project was financed by INRA Métaprogramme ACCAF and ERA.Net RUS. My PhD salary was paid by INRA and Bordeaux Sciences Agro.

Mark, Delphine, Bernd and Pavel, I hope I satisfied most of the selection criteria you defined a few years ago. I remember a PhD thesis offer (I bet Mark wrote this) and a Skype meeting both of a very high level (of attractiveness). Yes, I did survive day and night from -25 *to* $+30\,^{\circ}\mathrm{C}$. *I cope with hordes of bloodthirsty mosquitoes. I dragged on a few kilometres a heavy blowing machine in the snow, over the rail-road (OK, we did it with Anton, and I was there once on about 8 snow manipulations). And I like cows. However, I stayed rather reasonable on vodka and I did not have the occasion to run away from a bear (it might be better like that). Instead, we camped on a crime scene (hopefully, we learned that later on), we drove at high speed on country roads, sometimes in the roadside, and I endured fully naked "banya" sessions with "venik" (also with great pleasure). But this is an easy feeding of the fantasy many Western Europeans have on Siberia. Among the normal life things that I will remember from south-western Siberia are the welcoming people, some of their crazy life stories, landscapes, good food (soups, "chachlik", "gretchka", "piroschka", "salade Olivier", dried fish, "sala" and garlic, "pelmeni", etc.), but also a hardened apple and a frozen chicken in The container…*

Contents

List of Tables

List of Figures

Chapter 1

Introduction

1.1 Context

1.1.1 General features of Siberia

Siberia covers about 10 million km^2 in Northern Eurasia, or about 7 % of the global terrestrial land (Groisman et al. 2012a). As such, Siberia has a paramount influence on the regulation of global environmental processes. In particular, Siberian ecological features have strong feedbacks on global climate and biogeochemical cycles—i.e. fluxes of energy and matter between abiotic and biotic compartments—(Goetz et al. 2007; Groisman et al. 2012a; McGuire et al. 2007). Ranging from 45 to 75 ° N of latitude, Siberia ensures a large diversity of natural conditions, climate, soils, ecosystems, and landscapes (Shvidenko et al. 2012). From south to north, several bioclimatic zones have been defined on the basis of regional climate characteristics and vegetation community composition: steppe, forest-steppe, sub-taiga, southern taiga, middle taiga, northern taiga, forest tundra and tundra (Fig. 1.1). The taiga zones—different combinations of coniferous evergreen and deciduous tree species—represent about 77 % of the total area of Siberia (Shvidenko et al. 2012). Along with this gradient of environmental conditions, human land occupation varies. Agriculture has historically developed in the south of Siberia, in the steppe and forest-steppe zones, because the climatic conditions allow a longer and a warmer vegetation season and because the region concentrates fertile soils such as Chernozems (Groisman et al. 2012a; Shvidenko et al. 2012). Approximately 27 % of the currently occupied arable lands of the Russian Federation are located in the south of Siberia (Oldfield 2006). Populations mostly settled in this area which now concentrates the main Siberian cities and communication axes such as the Trans-Siberian Railway linking Moscow to the Pacific coast. In the north of the forest-steppe zone are huge repositories of natural resources: fossil fuels (natural gas, coal, oil), ore deposits, and forests (Groisman et al. 2012a). Siberian forests represent about 65 % of the total Russian forest area (Fomchenkov et al. 2003). They constitute a huge carbon repository and sink on the global scale (Dolman et al. 2012; Schaphoff et al. 2013; Shvidenko et al. 2012).

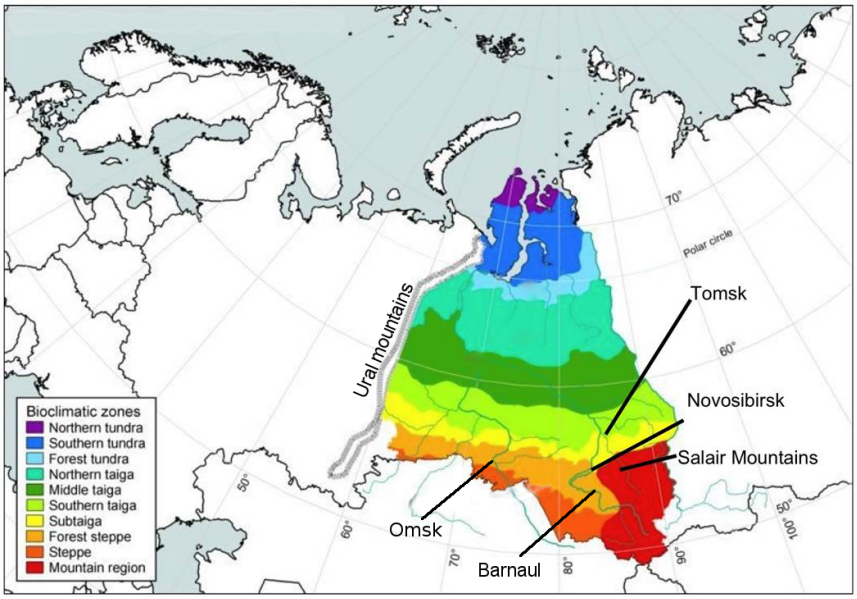


Figure 1.1: Bioclimatic zones of Western Siberia. Our study focussed on south-western Siberia, i.e. in the transition from steppe to southern-taiga.

1.1.2 Observed and projected climate change

Northern Eurasia, and particularly Siberia, experiences fast and intense climate change (Fig. 1.2; Groisman et al. 2012b; IPCC 2013). In the last century, mean annual surface air temperature rose by about 1.39 °C in Siberia, which is higher than over Northern Eurasia (+1.29 °C), the Arctic (+1.28 °C), or the entire northern hemisphere (+0.77 °C) (Groisman et al. 2012b). The warming trend over Northern Eurasia was particularly strong in the cold season (November to March) (IPCC 2013). Changes in precipitation were more variable regionally, were not regular in time, and diverged between seasons. For example, annual precipitations were higher by about 10 % in the second than in the first half of the twentieth century, but the subsequent changes were subtle. While precipitation amounts and the number of days with precipitation did not change in the further decades, a significant redistribution by intensity among the days with precipitation occurred in the warm season (Groisman et al. 2012b). For example, prolonged no-rain episodes (30 days and above) in summer were detected in the south of Siberia. An increase in the cold season precipitation occurred over most of Siberia (IPCC 2013; Rawlins et al. 2010). Altogether, maximum snow depth, the number of days with more than 20 cm snow as well as the snow water equivalent have increased in the last decades over most of Siberia (Bulygina et al. 2011, 2010, 2009). Snow cover extent over Siberia did not appreciably change during winter (December–March) but it significantly retreated in spring–early summer, from April to June (Fig. 1.3; Arndt et al. 2010; Bulygina et al. 2009; Groisman et al. 1994, 2006;

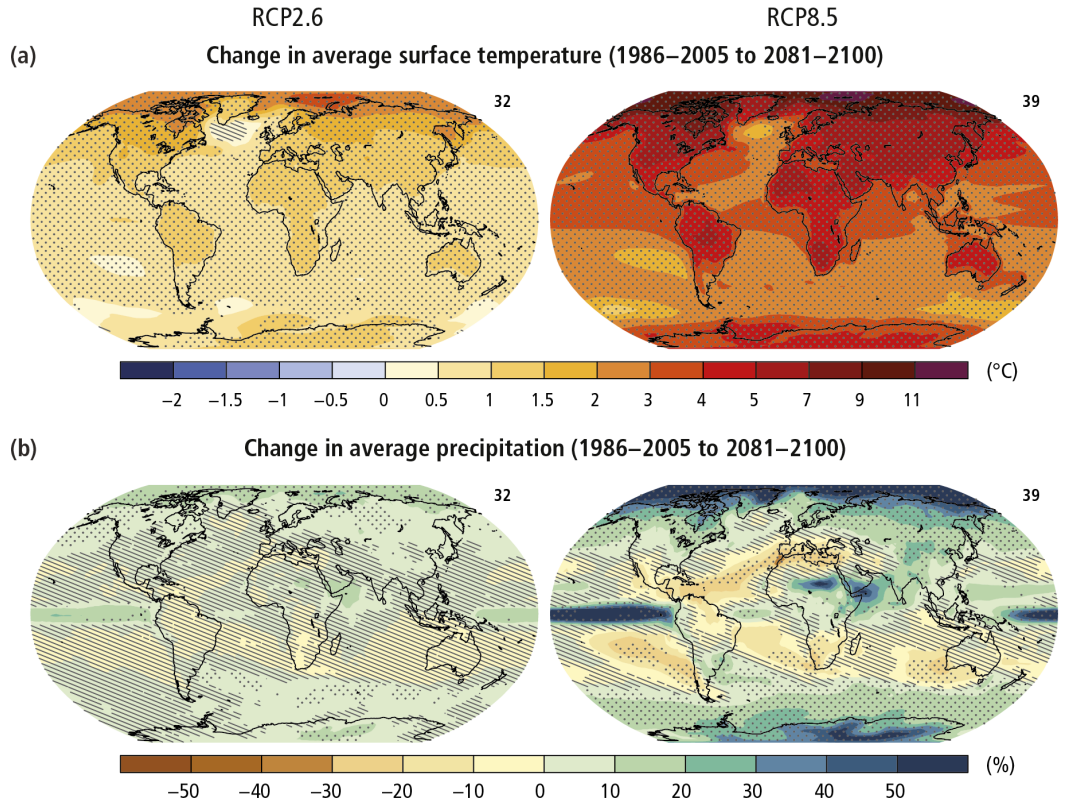


Figure 1.2: Change in average surface temperature (a) and change in average precipitation (b) based on multi-model mean projections for 2081–2100 relative to 1986–2005 under the RCP2.6 (left) and RCP8.5 (right) scenarii. The number of models used to calculate the multi-model mean is indicated in the upper right corner of each panel. Stippling (i.e., dots) shows regions where the projected change is large compared to natural internal variability and where at least 90 % of models agree on the sign of change. Hatching (i.e., diagonal lines) shows regions where the projected change is less than one standard deviation of the natural internal variability. ***Source:*** IPCC 2013.

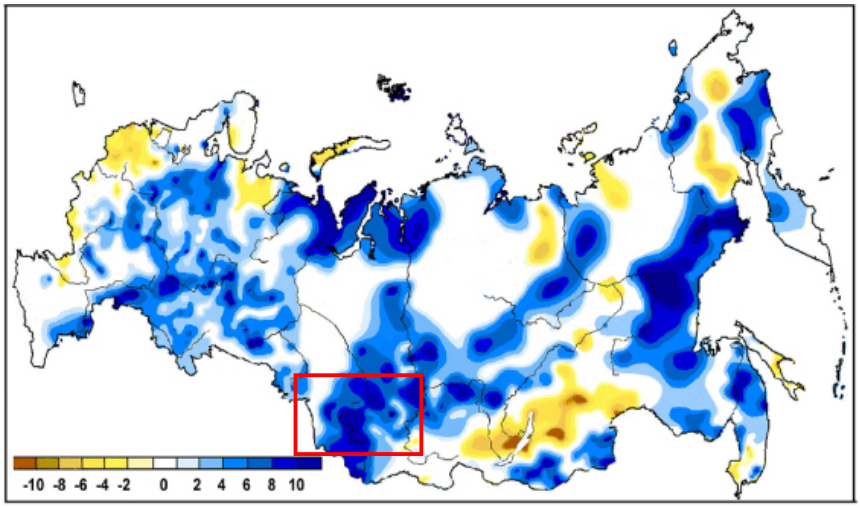


Figure 1.3: Spatial distribution of linear trend coefficients (days/10 year; 1–5 % significance level) showing the number of days with snow cover exceeding 20 cm for 1966–2007. Our study area is highlighted in red. ***Source:*** Bulygina et al. 2009.

Robinson et al. 1993; Takala et al. 2009).

Climate projections for Northern Eurasia indicate a further increase of surface air temperatures: between +2 and +9 °C in December–February and between +2 and +6.5 °C in June–August by the end of the 21st century in comparison with the 1986–2005 mean (Fig. 1.2; IPCC 2013). Annually, the largest temperature changes are expected in the polar region because of the preponderance of winter changes. However, in summer, the largest changes are expected to occur along a gradient towards the south of the region (Groisman et al. 2012b). Precipitations are also predicted to rise on the continental scale, but there is a greater uncertainty in the projections. October–March precipitations for Northern Eurasia are predicted to rise by 2–7 % by the end of the century, in comparison with the 1986–2005 mean, and April–September precipitations to rise by 5–15 % (IPCC 2013). However, changes in the frequency and intensity of precipitation events might be altered. Altogether, over most parts of Siberia, winter precipitations are expected to be more frequent and intense, hence increasing snow depth, while the precipitation rate may change slightly in summer, but precipitation events may become less frequent and more intense in this season (Groisman et al. 2012b).

Finally, in addition to mean value changes, the frequency and the intensity of extreme climate and weather events are likely to be modified during the 21st century (Groisman et al. 2012b; IPCC 2013). Overall, the number of record days with extremely low temperature will continue to decrease while the number of days with extremely high temperature will continue to increase (Meleshko et al. 2008).

1.1.3 Environmental impacts of global change in Siberia

Because of global change, substantial reshaping of Siberian ecosystems are expected (Groisman and Gutman 2012). Vegetation distribution and productivity will be modified and so land-use possibilities. Several factors control the composition of vegetation communities and productivity among which climate, soil, and disturbances.

In northern latitudes (e.g. boreal forest), it is usually assumed that vegetation growth is limited by short growing season, low growing season temperature, low solar radiation, and low nitrogen (N) availability (Boisvenue and Running 2006). Regionally, water availability and the seasonality of precipitations are also regulators of vegetation growth in Siberia (Berner et al. 2013; Boisvenue and Running 2006; Devi et al. 2008; Kharuk et al. 2006). Observation studies have reported a wide range of productivity variation with recent global change in Siberia (Schaphoff et al. 2016). For instance, the productivity of Russian boreal forests was found to be enhanced by increasing radiation (Berner et al. 2013; Ichii et al. 2013; Myneni et al. 1997), increasing atmospheric CO_2 concentrations (Ichii et al. 2013; Kharuk et al. 2011; Kharuk et al. 2014), or lengthening of the growing season (Berner et al. 2013; Ichii et al. 2013; Jeong et al. 2011; Myneni et al. 1997). However, it was reduced by heat waves (Bastos et al. 2014), and drought stress (Kharuk et al. 2013; Shvidenko et al. 2012). The effects of water-availability, positive or negative, were found to be season dependent (Berner et al. 2013; Devi et al. 2008; Kharuk et al. 2006).

In addition to climate or atmospheric factors, several abiotic and biotic disturbance factors have a great importance for the functioning of Siberian ecosystems. Among these factors, fires (e.g. forest fires, ground fires), pests (e.g. defoliator insects) and diseases (e.g. fungi) are changing along with climate. In fact, warmer and drier conditions have already increased, and are predicted to further intensify, fire frequency and intensity in Siberia (Groisman et al. 2007; Malevskii-Malevich et al. 2007; Mokhov and Chernokulsky 2010; Shkol'nik et al. 2008; Shvidenko et al. 2012; Soja et al. 2007). Warmer and drier weather allow larger scale insect outbreaks and the apparition of new species. Insect outbreaks may increase in intensity and frequency, notably in northern areas where colder and wetter conditions used to prevent them, but also because of decreasing resilience of ecosystems and disruption of community interactions (Shvidenko et al. 2012; Soja et al. 2007; Stireman et al. 2005).

Taken together, the recent changes in productivity were region- and tree species-specific, which is probably explained by local combinations of factors (Schaphoff et al. 2016). Simultaneous or sequential (on a short period) combinations of these factors are likely to accelerate and intensify the changes in ecosystem composition and functioning (Shvidenko et al. 2012).

As a consequence of climate change, the distribution of vegetation communities

will be modified. Observations revealed that treelines are already moving towards higher altitudes in many Siberian mountains (Soja et al. 2007). Projections with bioclimatic models, indicate for the 21st century that all bioclimatic zones could shift northwards, with a redistribution of their relative size (Fig. 1.4; Jiang et al. 2012; Kicklighter et al. 2014; Lucht et al. 2006; Shuman et al. 2015; Soja et al. 2007; Tchebakova et al. 2009, 2010). In particular, steppe, forest-steppe, and sub-taiga zones may spread over larger areas, at the expense of taiga zones, and tundra ecosystems may be constrained to small and local areas in the Arctic polar circle. All the climate scenarii tested by Tchebakova et al. (2009) indicate substantial changes from the 2020s. Overall, vegetation shifts are expected to remain moderate under 2–3 °C warming but to be substantial above.

Besides vegetation redistributions, bioclimatic models predict an increase in the area suitable for agriculture during the 21st century in Siberia. Tchebakova et al. (2011) tested different climate scenarii from IPCC (2007) and their impact for the growing conditions of several crops. They reported that 50–85 % of Central Siberia could become suitable for agriculture by the end of the century (Fig. 1.5). Also, depending on the suitability of soils, which was not included in the bioclimatic model they used, the traditional Siberian crops may expand as far as 500 km northwards (50–70 km decade^{-1}) and new species could be introduced in the south. However, drier conditions, will probably require irrigation in the south or even impede agriculture. In conjunction to vegetation shifts induced by climate, Kicklighter et al. (2014) tested the effect of land-management on future land-use possibilities. They reported, under a "business as usual" scenario (i.e. no climate-policy), that climate-induced vegetation shifts may allow expansion of areas devoted to food crop production (15 %) and pastures (39 %) over the 21st century. Under a climate stabilization scenario (i.e. with climate-policy consisting in a carbon tax applied to fossil fuel emissions), climate-induced vegetation shifts may permit expansion of areas devoted to biofuel production (25 %) and pastures (21 %), but reduce the expansion of areas devoted to food crop production by 10 %. In both scenarii, vegetation shifts are predicted to further reduce the areas devoted to timber production by 6–8 %.

All these environmental changes (vegetation productivity, vegetation distribution and disturbances) are likely to impact energy, carbon and water fluxes in Siberia. Also, because of feedback mechanisms, they are susceptible to impact on climate. In fact, ecosystems influence surface climate through their impact on radiation, energy, water and carbon fluxes. For example, boreal forest has a relatively low albedo in comparison with tundra (mix of shrub and grasses) and permanently snow-covered areas. Seasonal melting of snow-cover in Arctic and replacement of most of tundra areas by forest may increase regional and global temperatures (Foley et al. 2003). As stressed out by Kicklighter et al. (2014), who simulated the influence of climate-induced vegetation shifts on future land use and associated land carbon fluxes, consistent climate-policies are likely to be a key component for the mitigation

of global change impacts in Northern Eurasia. Notably, their simulations indicate that without climate-policy, ecosystem changes will be higher and Northern Eurasia may turn into a source of atmospheric carbon. On the contrary, climate-policy would attenuate environmental changes and maintain Northern Eurasia as a small carbon sink.

Due to the huge size of Siberia on the global scale, ecological processes occurring there have a global impact. Thus, understanding these processes may help improving projections on the future status of regional ecosystems and planning alternative and sustainable land-uses, and also to improve global change projections on the scale of the Earth system. Even though there is an increasing interest in the study of Siberian ecosystems, functional ecological data remain sparse in the international literature (Gordov and Vaganov 2010; Groisman and Soja 2009).

1.1.4 Focus on south-western Siberia

Among the general objectives mentioned above, there is a particular interest in determining the drivers of primary productivity in SW Siberia. In fact, this region is known for its potential for agriculture but the underlying mechanisms remain unclear, and so the evolution of this potential in the context of global change.

Focussing on south-western (SW) Siberia, our broad objective was to contribute characterizing the climate control on vegetation growth in order to improve projections on primary productivity in the context of global change. In particular, we were interested in the availability of resources, water and nutrients, and their climate-driven dynamics.

SW Siberia is located on the transition between the steppe and southern-taiga bioclimatic zones (Fig. 1.1). An obvious feature is the gradient in forest structure and composition. From the south to the north of SW Siberia, forest patches increase in size and number, with wider and more continuous forest areas in the north. With the increase in forest cover, grassland areas become sparser towards the north. Also, the distribution of vegetation species varies in SW Siberia (Fig. 1.6). This distribution is the reflect of a gradient of climate, soil, and anthropogenic influence.

The region is characterized by a cold-temperate climate with cold winters and relatively warm summers. Mean annual temperature ranges from about 0.8 °C in the north to about 3 °C in the south. The mean winter temperature ranges from −18 °C, in the north, to −14 °C, in the south, and the mean summer temperature from 17 to 20 °C. Temperature punctually reaches extremes below −45 °C, in winter, and above 30 °C, in summer. This gradient of temperature promotes longer vegetation season in the south. Mean annual precipitation ranges from less than 300 mm in the south (steppe) to about 600 mm in the north (southern-taiga). Winter is characterized by a seasonally permanent snow cover lasting several months. Both snow-pack duration and height increase in a south to north gradient: the snow-pack (> 1 cm)

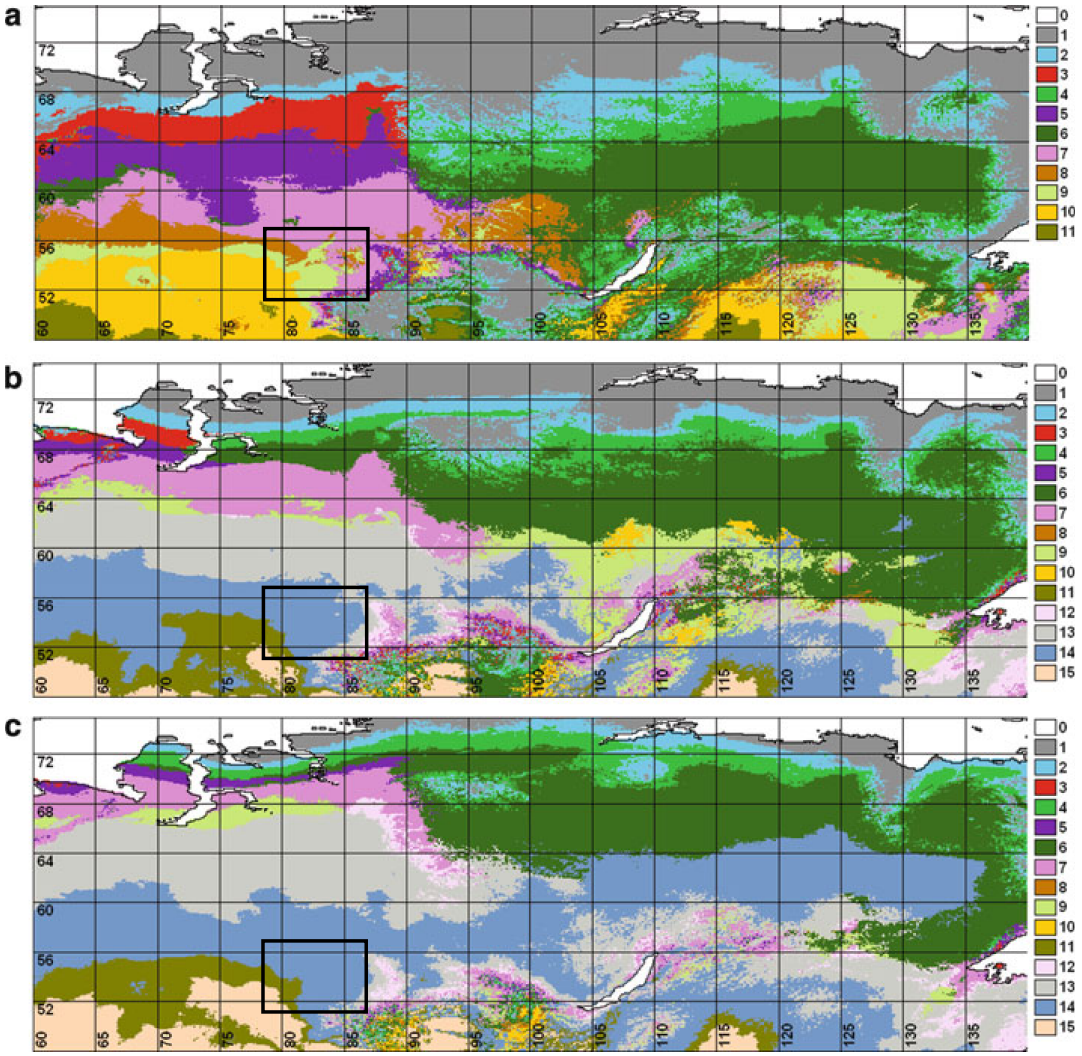


Figure 1.4: Vegetation distribution in Siberia in 2080 predicted from current climate (a), the moderate HadCM3 B1 (b) and the harsh A2 (c) climate change projections. Our study area is highlighted in black. Vegetation class key: (0) Water; (1) Boreal Tundra; (2) Forest-Tundra; (3) Northern Taiga-dark; (4) Northern Taiga-light; (5) Middle Taiga-dark; (6) Middle Taiga-light; (7) Southern Taiga-dark; (8) Southern Taiga-light; (9) Sub-taiga, Forest-Steppe; (10) Steppe; (11) Semi-desert; (12) Temperate Broadleaf; (13) Forest-Steppe; (14) Steppe; (15) Desert. ***Source:*** Shvidenko et al. 2012.

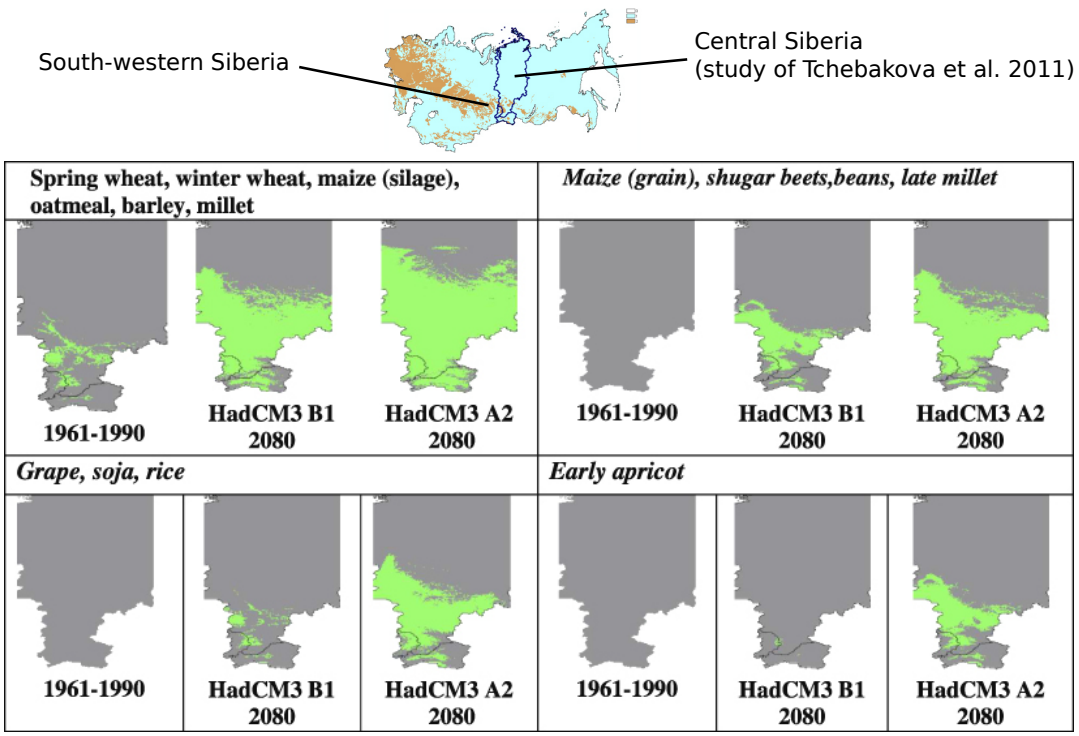


Figure 1.5: Potential climatic ranges (green) of traditional and new crop (italic) species in central Siberia in the 2010 and HadCM3 B1 and A2 2080 climates. ***Source:*** Tchebakova et al. 2011.

Figure 1.6: Map of the land cover type and forest species of Russia. Our study area is highlighted in black. ***Source:*** Schepaschenko et al. 2011.

lasts for about 130 days in the south and 180 days in the north and its depth between mid-February and mid-March (climax period) reach on average 15 cm in the south and 80 cm in the north.

Most of SW Siberian soils have developed on a common loess parent material deposited in the Quaternary (Chlachula 2003; Muhs 2007). However, the diverging climatic conditions, in interaction with vegetation cover features, induced diverging soil-forming processes. In the south, typically in the forest-steppe zone, the main soil-forming processes are the formation and accumulation of organic matter, leaching of carbonates in the topsoil and formation of secondary carbonates in deep soil layers. Soils belong to the groups of Chernozems and Phaeozems (Jones et al. 2009). In the north, typically in southern and sub-taiga, there are no Chernozems, Phaeozems are less frequent and Luvisols appear. The main soil-forming processes are related to the periodical movements of the water table, clays are washed from the topsoil and accumulate in the deeper layers and carbonates have disappeared from the first metre of the soil profile.

As previously mentioned, the south of Siberia has historically been more populated than the rest of Siberia and the south-west concentrates the highest population density. This has to be related to climatic conditions (longer and warmer vegetation season in the south of Siberia) and the presence of rich soils (typically Chernozems), which are more favourable for agriculture than in the rest of Siberia. As a con-

sequence of global change, agriculture may become possible on new and wider areas (Kicklighter et al. 2014; Tchebakova et al. 2011). However, the models developed until now to make such projections do not consider all components of site fertility, which integrates the dynamics of climatic conditions and resources availability (water and nutrients) necessary for plant growth (Chapin et al. 2011; Schoenholtz et al. 2000; Wardle 2004).

1.2 Objectives of the study and methods

Only a few ecological data are available for SW Siberia and we did not have access to long-term experimental sites, neither to sites which would have already been studied. Thus, the present work consisted in the selection and the characterization of sites with the objective of identifying factors and processes involved in the control of vegetation growth. In particular, we focussed on the relations between climate and the availability of resources (water and nutrients) for plants.

Site fertility integrates the dynamics of climatic conditions and resources availability (water and nutrients) required for plant growth (Schoenholtz et al. 2000). In a lot of ecosystems, nutrient limitation is rather an issue of real availability for plants than presence (Giehl and Wiren 2014). An important ecosystem compartment in the control of fertility is soil, which is considered as the main repository of nutrients and water for plant uptake. Water storage and availability are mainly dependent on soil physical properties (e.g. texture, structure) while nutrient availability is more dependent on soil chemical and biological properties. The size of the pool of available nutrients (soil solution and exchangeable/available pools) at a given time is of importance, but the processes that may replenish or flush this pool over time must also be considered (e.g. weathering, atmospheric deposition, nutrient leaching, biological cycling) (Legout et al. 2014; Ranger and Turpault 1999).

Whenever possible, we stressed on snow effects since this variable is an important feature of Siberian ecosystems and its levels tend to rise with global change, by contrast with most of the other regions of the world. Snow controls winter soil thermal regime because of its insulation properties. In cold ecosystems, such as Siberia, the soil temperature under the snow-pack can be completely decoupled from air temperature and the soil can be protected from freezing (Zhang 2005). Soil freezing is known to greatly reduce biological activity (soil fauna and microorganisms) by physiological control, impeding movements because of changes in the physical properties of the environment, or because it reduces water availability, which is a pre-requisite for microbial activity (Davidson and Janssens 2006; Öquist et al. 2009). Natural or experimentally induced snow gradients were found to influence winter microbial and enzymatic activities, and so organic matter mineralization and, by extension, the release of nutrients like nitrogen in a wide variety of ecosystems

(Brooks et al. 2011; Groffman et al. 2006; Grogan and Jonasson 2005; Jusselme et al. 2016; Monson et al. 2006; Schimel et al. 2004; Shibata et al. 2013). Seasonal snow-covers constitute a pool of water that is released to the soil at snow-melt. In SW Siberia, depending on the soil water content before the snow season, the melt-water may constitute an important input for the oncoming vegetation season because the precipitation levels are relatively low. In the same time, snow-melt could be associated with nutrient loss (for example, by leaching of nitrogen and phosphorus; Ågren et al. 2010; Hardy et al. 2001; Sebestyen et al. 2008; Yano et al. 2015).

This PhD thesis has been organized around five axes (Chap. 3–7) which are described below.

1.2.1 Relation between tree-growth and climate in contrasting pedoclimatic situations

The relations between climate and tree growth can be approached through dendrochronological methods. Essentially, the measure of tree ring-width provides two kinds of information: the average radial growth level of a tree and the inter-annual variations of its growth. While the average growth level is an integration of internal (age) and environmental conditions (e.g. average climate, topography, soil, competition, management), the inter-annual variation of tree ring-width is the result of varying climatic conditions and/or disturbances (e.g. insect outbreaks, fire, hurricane) (Cook and Kairiukstis 1990; Fritts 1976). Climate controls tree growth through its regulation of eco-physiological processes (which depend notably on light, temperature, and water availability) but also through its impact on the physical, chemical and biological processes involved in the release of plant-available nutrients in the ecosystem.

In addition, the climate–growth relations are not well known for *Populus tremula* L., a tree species commonly found in SW Siberia (Schepaschenko et al. 2011) and which could spread in new areas of Northern Eurasia in the 21st century (Shuman et al. 2015). Although the study of the relations between tree ring-width and air temperature and precipitation have historically been the focus of most studies, the relations with other parameters, and particularly snow, are less common.

We addressed the following questions: (1) *How does climate regulate tree growth in contrasting pedoclimatic conditions in SW Siberia?* (2) *In particular, has snow a noticeable influence on tree growth?* and (3) *Has average tree growth changed in the recent decades?*

Since SW Siberia is positioned on a gradient of climate and soil processes, we hypothesized that tree growth responds to different climatic parameters depending on their position in the region. Concretely, high temperatures might alleviate a tree growth limitation in the northern part of SW Siberia while it could be associated

with water limitation in the south. Also, years with relatively high snow levels may enhance tree growth in the southern zone, because of increased water availability. Finally, in the last decades, it is possible that the average tree growth was enhanced if global change (temperature, precipitation, CO_2 levels, nitrogen deposition, etc.) was sufficient to alleviate growth limitations, or reduced if global change exacerbated existing limitations or induced new ones.

To test our hypotheses, we measured tree ring-width on six sites of SW Siberia presenting contrasting pedoclimatic situations. Standard chronologies were built for each site and related to local climatic parameters with dendrochronological procedures (Chap. 3).

1.2.2 Soil temperature and moisture regimes and their potential evolution with climate variations in two contrasting pedoclimatic situations

Soil temperature and moisture regimes control biological activity, from the soil fauna and micro-organisms, that are responsible for the decomposition of organic matter and thus the release of nutrients, to the plant and its symbiotic partners, which are taking up resources. Because of their influence on nutrient availability (e.g. through decomposition and mineralization processes, mass flow, diffusion) and on the physiology of uptake systems (e.g. fine roots, mycorrhizae, stomata aperture), altered temperature and water availability, either in deficit or in excess, impair the mineral nutrition of plants (Bassirirad 2000; Kreuzwieser and Gessler 2010; Rennenberg et al. 2009). Soil temperature and moisture regimes are the result of climatic conditions and are thus dynamic across the seasons. In addition, they are greatly modulated by soil properties as well as by soil cover properties (e.g. vegetation type and density, presence of snow). Properties of the soil cover control the fluxes of energy (e.g. albedo) and matter (e.g. water interception, evapo-transpiration) to and from the soil.

In the Chap. 4 of this manuscript, we address the following questions: (1) *What are the current soil temperature and moisture regimes in forest-steppe and sub-taiga?* and (2) *How are climate variations, and in particular snow depth, susceptible to influence these regimes in contrasting pedoclimatic situations?*

To reach these goals, we recorded the dynamics of soil temperature and moisture under aspen forest and grassland vegetation covers in two contrasting sites of SW Siberia. The impact of snow cover on these dynamics was assessed by manipulating its height in the field and also through the modelling of soil water budget with the model Biljou (Granier et al. 1999). To assess the potential effects of climate change on the soil water budget, we performed simulations with modified climatic conditions. Essentially, we tested the simultaneous effects of higher temperatures,

drier summer conditions and varying snow amounts in winter.

1.2.3 Fine root soil exploration in contrasting pedoclimatic situations

Fine roots (usually defined by a diameter < 2 mm), with or without symbiotic partners (ecto-mycorrhizae, endo-mycorrhizae, bacteria), are responsible for most of nutrient and water acquisition. They play a crucial role in the cycling of carbon and nutrients in forest ecosystems (Berg 1984; Helmisaari et al. 2002; Hendrick and Pregitzer 1993; Joslin and Henderson 1987; Leppälammi-Kujansuu et al. 2014).

On the global scale, general patterns of fine root distribution within the soil profile have been reported in relation to the distribution of terrestrial biomes (Jackson et al. 1997). Fine root distribution and dynamics (production, turnover, life history) respond to environmental factors such as stand characteristics (e.g. species, age, density), soil properties (e.g. nutrient stocks, pH) and climatic features (Finér et al. 2011; Gill and Jackson 2000; Hendricks et al. 2006; Joslin et al. 2000; Leuschner and Hertel 2003; McCormack et al. 2014, 2013; McCormack and Guo 2014; Yuan and Chen 2010, 2012a,b).

We aimed to identify general fine root patterns, important for plant nutrition and thought to be sensitive to climate changes in SW Siberia. The distribution of fine roots throughout the soil profile is a good proxy to start assessing the environmental constraints (physical and/or chemical) for the mining of their resources (water and nutrients) by plants. In the Chap. 5, we address the following question: *Do contrasting climate and soil conditions lead to diverging fine root distributions in SW Siberia?*

To answer this question, we measured fine root length and mass down to 1 m depth, in aspen forests and grasslands, at six sites presenting different soil and climatic conditions.

1.2.4 Assessment of nitrogen and phosphorus status

Nutrient availability is a key regulator of primary productivity and carbon balance of ecosystems (Chapin et al. 2011; Fernández-Martínez et al. 2014; Wieder et al. 2015). Nutrient availability varies both in space and time, and this variability can ultimately be more important for vegetation growth than the changes in plant physiology driven by climate (Lukac et al. 2010; Salih et al. 2005). Eventually in interaction with other environmental factors, such as water availability, limited nutrient availability can counter-balance the growth enhancement by rising atmospheric CO_2 concentration (Norby et al. 2010; Oren et al. 2001; Reich et al. 2014; van Groenigen et al. 2006).

Either individually or in combination, nitrogen (N) and phosphorus (P) are the major nutrients commonly found to constrain biological processes and primary

productivity (Elser et al. 2007; Fay et al. 2015; Güsewell 2004; Harpole et al. 2011; LeBauer and Treseder 2008; Vitousek et al. 2010). Nitrogen and phosphorus enter ecosystems via geologic and atmospheric pathways. Then, they are recycled through the plant–soil–microbe system via organic matter decomposition processes (Aerts and Chapin 1999; Attiwill and Adams 1993; Chapin et al. 2011). The increase of atmospheric CO_2 concentration and N deposition, which are in general stronger and faster than any P input, are modifying the CNP stoichiometry of ecosystems (Peñuelas et al. 2013). As a consequence, a progressive shift from N limitation to P limitation or a N-P co-limitation can occur (Ågren et al. 2012; Peñuelas et al. 2012; Vitousek et al. 2010). These modifications of biogeochemical cycling on global and regional scales will participate in the way ecosystem reshaping is driven, for example through the modification of plant communities adapting to new stoichiometric constraints (Güsewell 2004). It may also have consequences for agricultural potential on these scales.

Soil phosphorus status in contrasting pedoclimatic situations

Most of the P that is bio-available in ecosystems originates from the weathering of the soil mineral phase and/or by the recycling of organic matter. Along with soil development, the mineral phase is depleted, P becomes increasingly limiting and the recycling of organic P forms is of increasing importance for plant growth (Walker and Syers 1976).

Phosphorus is bio-available in the soil in the form of phosphate ions (mostly $H_2PO_4^-$ and HPO_4^{2-}; Lindsay 1979). The availability of phosphate ions is mostly controlled by geochemical reactions because of their poor mobility and their high reactivity with soil components. Soil pH exerts a major control on the speciation of phosphate ions in the soil solution, their interactions with other ligands such as metal cations, and the precipitation–dissolution of P-containing complexes (Hinsinger 2001). Once free in solution, phosphate ions are electrostatically attracted to positively charged sites on clay minerals (on their edges), carbonates and organic matter (Gérard 2016; Hinsinger 2001; Parfitt 1978). The availability of phosphate ions can decrease when they form covalent bounds with metals, e.g. iron and aluminium oxides, or when they precipitate in mineral forms (Barber 1995). Through their action on soil pH and the exudation of organic acids/anions, roots enhance the bio-availability of P in the rhizosphere (Hinsinger 2001). The microbial biomass can also constitute a pool of immobilized P which can be easily made available (Bünemann et al. 2012; Oberson et al. 2001). Overall, the plant-availability of P in a soil depends for a great part on the capacity of the soil to exchange phosphate ions between the solid and the liquid phases.

It is often considered that P is not the main limiting nutrient in northern ecosystems (Hedin 2004; Reich and Oleksyn 2004). Also, P fertilization in agriculture is

barely, if not at all, practised in Siberia. However, a few assessments of P availability have been conducted in Northern Eurasia, and a reconsideration of such a paradigm might be necessary in the context of global change. We addressed the following questions in the Chap. 6: *What is the phosphorus status of SW Siberian soils?* and in particular, *Which amount of phosphorus is available for plants?*

At a given time, the characterization of the size of different P pools and of soil properties provide a good approximation of the potential importance of the geochemical and biological pathways. The quantification of the pool of isotopically exchangeable phosphate ions as function of time is a good proxy for the bio-availability of P in the ecosystem (Fardeau 1996; Frossard et al. 2011; Morel and Plenchette 1994).

Thus, we measured the size of different P pools in the soil of six sites of SW Siberia with contrasting climate and soil conditions: total P, inorganic P, organic P as well as, in standard conditions, phosphate ions in the soil solution and diffusive phosphate ions at the solid–solution interface as a function of time. Classical soil analyses were combined with an isotopic dilution kinetics method. The size of P pools assessed at Siberian sites were compared with a global data set compiled from 236 references.

Redistribution of the nitrogen derived from leaf litter decomposition within ecosystem compartments in contrasting pedoclimatic situations

Contrary to P, the N which is available for plants almost exclusively derives from the biological pathway. Atmospheric N_2 is initially integrated in the living biomass by N-fixers (bacteria and archae, eventually in symbiosis with plants), which transform it into reactive N (Cleveland et al. 1999; Galloway et al. 2004). Most plants take up N in the soil solution either in organic (amino-acids) or inorganic (ammonium, NH_4^+; nitrate, NO_3^-) forms (Näsholm et al. 2009; Schimel and Bennett 2004).

The N in the soil solution mainly originates from decomposition processes, which consist in fragmentation, depolymerization and mineralization of litter and soil organic matter (Schimel and Bennett 2004). Above- (e.g. dead leaves and branches) and below-ground (dead roots) litter inputs are thus key components of N cycling in terrestrial ecosystems. Aerial litter decomposition is controlled by climate, decomposer activity, and its inherent chemical composition (Berg and McClaugherty 2014). During the process of litter decomposition, which is carried out by complex interactions between abiotic (light, wind, temperature, precipitation, freezing, etc.) and biotic factors (soil fauna, fungi and bacteria), litter is broken down into smaller sized particles and soluble compounds (Berg and McClaugherty 2014). These products of litter decomposition are incorporated to the mineral soil and become soil organic matter (SOM). Depending on environmental conditions—such as soil properties, soil processes, biological activity and climatic conditions—SOM follows different pathways of mineralization and/or stabilization (Cotrufo et al. 2015; Lehmann and Kleber 2015; Schmidt et al. 2011; von Lützow et al. 2006).

SW Siberian soils are formed on a common loess deposit but they are submitted to different climatic conditions. In the south, typically in steppe/forest-steppe, soil experiences freezing over winter because of a relatively shallow snow-pack, and water shortages are frequent in summer. In the north, typically in sub-taiga, the soil is barely frozen in winter due a thick snow-pack and soil moisture content is not limiting in summer.

In the respective chapter (Chap. 7), we addressed the following questions: *Is the liberation of nitrogen from the leaf-litter driven by climatic conditions? Is the fate of N in the soil controlled by climate?*

To answer these questions, we tracked leaf-derived N over time in the soil–plant continuum using ^{15}N labelling in four sites presenting different climate.

References

Aerts, R. and Chapin, F. (1999). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. In: *Advances in Ecological Research*, 1–67. DOI: 10.1016/s0065-2504(08)60016-1.

Ågren, A., Haei, M., Köhler, S. J., Bishop, K., and Laudon, H. (2010). Regulation of stream water dissolved organic carbon (DOC) concentrations during snowmelt – the role of discharge, winter climate and memory effects. *Biogeosciences* 7.9, 2901–2913. DOI: 10.5194/bg-7-2901-2010.

Ågren, G. I., Wetterstedt, J. Å. M., and Billberger, M. F. K. (2012). Nutrient limitation on terrestrial plant growth - modeling the interaction between nitrogen and phosphorus. *New Phytologist* 194.4, 953–960. DOI: 10.1111/j.1469-8137.2012.04116.x.

Arndt, D. S., Baringer, M. O., and Johnson, M. R. (2010). State of the Climate in 2009. *Bulletin of the American Meteorological Society* 91.7, s1–s222. DOI: 10.1175/bams-91-7-stateoftheclimate.

Attiwill, P. M. and Adams, M. A. (1993). Tansley Review No. 50. Nutrient cycling in forests. *New Phytologist* 124.4, 561–582.

Barber, S. A. (1995). Soil nutrient bioavailability – A mechanistic approach. In: 2nd. Chap. 9: Phosphorus, 201–228.

Bassirirad, H. (2000). Kinetics of nutrient uptake by roots: responses to global change. *New Phytologist* 147.1, 155–169. DOI: 10.1046/j.1469-8137.2000.00682.x.

Bastos, A., Gouveia, C. M., Trigo, R. M., and Running, S. W. (2014). Analysing the spatio-temporal impacts of the 2003 and 2010 extreme heatwaves on plant productivity in Europe. *Biogeosciences* 11.13, 3421–3435. DOI: 10.5194/bg-11-3421-2014.

Berg, B. (1984). Decomposition of root litter and some factors regulating the process: Long-term root litter decomposition in a scots pine forest. *Soil Biology and Biochemistry* 16.6, 609–617. DOI: http://dx.doi.org/10.1016/0038-0717(84)90081-6.

Berg, B. and McClaugherty, C. (2014). *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*. Third Edition. Springer Science + Business Media. DOI: 10.1007/978-3-642-38821-7.

Berner, L. T., Beck, P. S. A., Bunn, A. G., and Goetz, S. J. (2013). Plant response to climate change along the forest-tundra ecotone in northeastern Siberia. *Global Change Biology*. DOI: 10.1111/gcb.12304.

Boisvenue, C. and Running, S. W. (2006). Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. *Global Change Biology* 12.5, 862–882. DOI: 10.1111/j.1365-2486.2006.01134.x.

Brooks, P. D., Grogan, P., Templer, P. H., Groffman, P., Öquist, M. G., and Schimel, J. (2011). Carbon and nitrogen cycling in snow-covered environments. *Geography Compass* 5.9, 682–699. DOI: 10.1111/j.1749-8198.2011.00420.x.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Korshunova, N. N. (2011). Changes in snow cover characteristics over Northern Eurasia since 1966. *Environmental Research Letters* 6.4, 045204. DOI: 10.1088/1748-9326/6/4/045204.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Radionov, V. F. (2010). Snow cover basal ice layer changes over Northern Eurasia since 1966. *Environmental Research Letters* 5.1, 015004. DOI: 10.1088/1748-9326/5/1/015004.

Bulygina, O. N., Razuvaev, V. N., and Korshunova, N. N. (2009). Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters* 4.4, 045026. DOI: 10.1088/1748-9326/4/4/045026.

Bünemann, E., Oberson, A., Liebisch, F., Keller, F., Annaheim, K., Huguenin-Elie, O., and Frossard, E. (2012). Rapid microbial phosphorus immobilization dominates gross phosphorus fluxes in a grassland soil with low inorganic phosphorus availability. *Soil Biology and Biochemistry* 51, 84–95. DOI: 10.1016/j.soilbio.2012.04.012.

Chapin, F. S., Matson, P. A., and Vitousek, P. M. (2011). *Principles of Terrestrial Ecosystem Ecology (Second Edition)*. Springer Science + Business Media. DOI: 10.1007/978-1-4419-9504-9.

Chlachula, J. (2003). The Siberian loess record and its significance for reconstruction of Pleistocene climate change in north-central Asia. *Quaternary Science Reviews* 22.18-19, 1879–1906. DOI: 10.1016/s0277-3791(03)00182-3.

Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., Perakis, S. S., Latty, E. F., Von Fischer, J. C., Elseroad, A., and Wasson, M. F. (1999). Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems. *Global Biogeochemical Cycles* 13.2, 623–645. DOI: 10.1029/1999GB900014.

Cook, E. R. and Kairiukstis, L. A., eds. (1990). *Methods of Dendrochronology*. Springer Science + Business Media. DOI: 10.1007/978-94-015-7879-0.

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M., Wall, D. H., and Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience* 8.10, 776–779. DOI: 10.1038/ngeo2520.

Davidson, E. A. and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440.7081, 165–173. DOI: 10.1038/nature04514.

Devi, N., Hagedorn, F., Moiseev, P., Bugmann, H., Shiyatov, S., Mazepa, V., and Rigling, A. (2008). Expanding forests and changing growth forms of Siberian larch at the Polar

Urals treeline during the 20th century. *Global Change Biology* 14.7, 1581–1591. DOI: 10.1111/j.1365-2486.2008.01583.x.

Dolman, A. J., Shvidenko, A., Schepaschenko, D., Ciais, P., Tchebakova, N., Chen, T., Molen, M. K. van der, Belelli Marchesini, L., Maximov, T. C., Maksyutov, S., and Schulze, E.-D. (2012). An estimate of the terrestrial carbon budget of Russia using inventory-based, eddy covariance and inversion methods. *Biogeosciences* 9.12, 5323–5340. DOI: 10.5194/bg-9-5323-2012.

Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10.12, 1135–1142. DOI: 10.1111/j.1461-0248.2007.01113.x.

Fardeau, J. (1996). Dynamics of phosphate in soils. An isotopic outlook. *Fertilizer Research* 45.2, 91–100. DOI: 10.1007/bf00790658.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., Collins, S. L., Davies, K. F., Du, G., Feng, X., Firn, J., Gruner, D. S., Hagenah, N., Hautier, Y., Heckman, R. W., Jin, V. L., Kirkman, K. P., Klein, J., Ladwig, L. M., Li, Q., McCulley, R. L., Melbourne, B. A., Mitchell, C. E., Moore, J. L., Morgan, J. W., Risch, A. C., Schütz, M., Stevens, C. J., Wedin, D. A., and Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants* 1.7, 15080. DOI: 10.1038/nplants.2015.80.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., III, F. S. C., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F., and Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4.6, 471–476. DOI: 10.1038/nclimate2177.

Finér, L., Ohashi, M., Noguchi, K., and Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* 262.11, 2008–2023. DOI: 10.1016/j.foreco.2011.08.042.

Foley, J. A., Costa, M. H., Delire, C., Ramankutty, N., and Snyder, P. (2003). Green surprise? How terrestrial ecosystems could affect earth's climate. *Frontiers in Ecology and the Environment* 1.1, 38–44. DOI: 10.1890/1540-9295(2003)001[0038:gshtec]2.0.co;2.

Fomchenkov, V., Sdobnova, V., Danilov, N., Danilova, S., Kurdina, G., and Beljakova, T. (2003). *Forest fund of Russia (Data of State Forest Account).* Tech. rep. All-Russia Research Institute of Forestry and Mechanization.

Fritts, H. C. (1976). *Tree rings and climate.* Academic Press, p. 567.

Frossard, E., Achat, D. L., Bernasconi, S. M., Bünemann, E. K., Fardeau, J.-C., Jansa, J., Morel, C., Rabeharisoa, L., Randriamanantsoa, L., Sinaj, S., Tamburini, F., and Oberson, A. (2011). The use of tracers to investigate phosphate cycling in soil–plant systems. In: *Phosphorus in Action.* Vol. 100, 59–91. DOI: 10.1007/978-3-642-15271-9_3.

Galloway, J., Dentener, F., Capone, D., Boyer, E., Howarth, R., Seitzinger, S., Asner, G., Cleveland, C., Green, P., Holland, E., Karl, D., Michaels, A., Porter, J., Townsend, A., and

Vöosmarty, C. (2004). Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70 (2), 153–226. DOI: 10.1007/s10533-004-0370-0.

Gérard, F. (2016). Clay minerals, iron/aluminum oxides, and their contribution to phosphate sorption in soils – A myth revisited. *Geoderma* 262, 213–226. DOI: 10.1016/j.geoderma.2015.08.036.

Giehl, R. F. H. and Wiren, N. von (2014). Root Nutrient Foraging. *Plant Physiology* 166.2, 509–517. DOI: 10.1104/pp.114.245225.

Gill, R. A. and Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147.1, 13–31. DOI: 10.1046/j.1469-8137.2000.00681.x.

Goetz, S. J., Mack, M. C., Gurney, K. R., Randerson, J. T., and Houghton, R. A. (2007). Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: observations and model results contrasting northern Eurasia and North America. *Environmental Research Letters* 2.4, 045031. DOI: 10.1088/1748-9326/2/4/045031.

Gordov, E. P. and Vaganov, E. A. (2010). Siberia integrated regional study: multidisciplinary investigations of the dynamic relationship between the Siberian environment and global climate change. *Environmental Research Letters* 5.1, 015007. DOI: 10.1088/1748-9326/5/1/015007.

Granier, A., Bréda, N., Biron, P., and Villette, S. (1999). A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* 116.2–3, 269–283. DOI: 10.1016/S0304-3800(98)00205-1.

Groffman, P. M., Hardy, J. P., Driscoll, C. T., and Fahey, T. J. (2006). Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. *Global Change Biology* 12.9, 1748–1760. DOI: 10.1111/j.1365-2486.2006.01194.x.

Grogan, P. and Jonasson, S. (2005). Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Global Change Biology* 11.3, 465–475. DOI: 10.1111/j.1365-2486.2005.00912.x.

Groisman, P. Y. and Gutman, G., eds. (2012). *Regional Environmental Changes in Siberia and Their Global Consequences*. Springer Science + Business Media. DOI: 10.1007/978-94-007-4569-8.

Groisman, P. Y., Gutman, G., Shvidenko, A. Z., Bergen, K. M., Baklanov, A. A., and Stackhouse Jr, P. W. (2012a). Intoduction: regional features of Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 1, 1–17. DOI: 10.1007/978-94-007-4569-8_1.

Groisman, P. Y., Blyakharchuk, T. A., Chernokulsky, A. V., Arzhanov, M. M., Marchesini, L. B., Bogdanova, E. G., Borzenkova, I. I., Bulygina, O. N., Karpenko, A. A., Karpenko, L. V., Knight, R. W., Khon, V. C., Korovin, G. N., Meshcherskaya, A. V., Mokhov, I. I., Parfenova, E. I., Razuvaev, V. N., Speranskaya, N. A., Tchebakova, N. M., and Vygodskaya, N. N. (2012b). Climate changes in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 3, 57–109. DOI: 10.1007/978-94-007-4569-8_3.

Groisman, P. Y., Karl, T. R., Knight, R. W., and Stenchikov, G. L. (1994). Changes of snow cover, temperature, and radiative heat balance over the northern hemisphere. *Journal of Climate* 7.11, 1633–1656. DOI: 10.1175/1520-0442(1994)007<1633:COSCTA>2.0.CO;2.

Groisman, P. Y., Knight, R. W., Razuvaev, V. N., Bulygina, O. N., and Karl, T. R. (2006). State of the ground: Climatology and changes during the past 69 Years over Northern Eurasia for a rarely used measure of snow cover and frozen land. *Journal of Climate* 19.19, 4933–4955. DOI: 10.1175/JCLI3925.1.

Groisman, P. Y., Sherstyukov, B. G., Razuvaev, V. N., Knight, R. W., Enloe, J. G., Stroumentova, N. S., Whitfield, P. H., Førland, E., Hannsen-Bauer, I., Tuomenvirta, H., Aleksandersson, H., Mescherskaya, A. V., and Karl, T. R. (2007). Potential forest fire danger over Northern Eurasia: Changes during the 20th century. *Global and Planetary Change* 56.3-4, 371–386. DOI: 10.1016/j.gloplacha.2006.07.029.

Groisman, P. and Soja, A. J. (2009). Ongoing climatic change in Northern Eurasia: justification for expedient research. *Environmental Research Letters* 4.4, 045002. DOI: 10.1088/1748-9326/4/4/045002.

Güsewell, S. (2004). N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164.2, 243–266. DOI: 10.1111/j.1469-8137.2004.01192.x.

Hardy, J. P., Groffman, P. M., Fitzhugh, R. D., Henry, K. S., Welman, A. T., Demers, J. D., Fahey, T. J., Driscoll, C. T., Tierney, G. L., and Nolan, S. (2001). Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56 (2), 151–174. DOI: 10.1023/A:1013036803050.

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B., and Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters* 14.9, 852–862. DOI: 10.1111/j.1461-0248.2011.01651.x.

Hedin, L. O. (2004). Global organization of terrestrial plant-nutrient interactions. *Proceedings of the National Academy of Sciences* 101.30, 10849–10850. DOI: 10.1073/pnas.0404222101.

Helmisaari, H.-S., Makkonen, K., Kellomäki, S., Valtonen, E., and Mälkönen, E. (2002). Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *Forest Ecology and Management* 165.1–3, 317–326. DOI: http://dx.doi.org/10.1016/S0378-1127(01)00648-X.

Hendrick, R. L. and Pregitzer, K. S. (1993). The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Canadian Journal of Forest Research* 23.12, 2507–2520. DOI: 10.1139/x93-312.

Hendricks, J. J., Hendrick, R. L., Wilson, C. A., Mitchell, R. J., Pecot, S. D., and Guo, D. (2006). Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology* 94.1, 40–57. DOI: 10.1111/j.1365-2745.2005.01067.x.

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* 237.2, 173–195. DOI: 10.1023/A:1013351617532.

Ichii, K., Kondo, M., Okabe, Y., Ueyama, M., Kobayashi, H., Lee, S.-J., Saigusa, N., Zhu, Z., and Myneni, R. (2013). Recent Changes in Terrestrial Gross Primary Productivity in Asia from 1982 to 2011. *Remote Sensing* 5.11, 6043–6062. DOI: 10.3390/rs5116043.

IPCC (2007). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor, and H. Miller. Cambridge University Press. 996 pp.

IPCC (2013). *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Ed. by T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. Midgley. Cambridge Books Online. Cambridge University Press. 1535 pp. DOI: 10.1017/CBO9781107415324.

Jackson, R. B., Mooney, H. A., and Schulze, E.-. D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* 94.14, 7362–7366. DOI: 10.1073/pnas.94.14.7362.

Jeong, S.-J., Ho, C.-H., Gim, H.-J., and Brown, M. E. (2011). Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982-2008. *Global Change Biology* 17.7, 2385–2399. DOI: 10.1111/j.1365-2486.2011.02397.x.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J. (2012). Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. *Ecology and Evolution* 2.3, 593–614. DOI: 10.1002/ece3.85.

Jones, A., Stolbovoy, V., Tarnocai, C., Broll, G., Spaargaren, O., and Montanarella, L., eds. (2009). *Soil Atlas of the Northern Circumpolar Region*. European Commission, Office for Official Publications of the European Communities, p. 142. DOI: 10.2788/95795.

Joslin, J. D. and Henderson, G. S. (1987). Organic matter and nutrients associated with fine root turnover in a white oak stand. *Forest Science* 33.2, 330–346.

Joslin, J. D., Wolfe, M. H., and Hanson, P. J. (2000). Effects of altered water regimes on forest root systems. *New Phytologist* 147.1, 117–129. DOI: 10.1046/j.1469-8137.2000.00692.x.

Jusselme, M.-D., Saccone, P., Zinger, L., Faure, M., Roux, X. L., Guillaumaud, N., Bernard, L., Clement, J.-C., and Poly, F. (2016). Variations in snow depth modify N-related soil microbial abundances and functioning during winter in subalpine grassland. *Soil Biology and Biochemistry* 92, 27–37. DOI: 10.1016/j.soilbio.2015.09.013.

Kharuk, V. I., Dvinskaya, M. L., Im, S. T., and Ranson, K. J. (2011). The Potential Impact of CO_2 and Air Temperature Increases on Krummholz Transformation into Arborescent Form in the Southern Siberian Mountains. *Arctic, Antarctic, and Alpine Research* 43.4, 593–600. DOI: 10.1657/1938-4246-43.4.593.

Kharuk, V. I., Ranson, K. J., Im, S. T., and Naurzbaev, M. M. (2006). Forest-tundra larch forests and climatic trends. *Russian Journal of Ecology* 37.5, 291–298. DOI: 10.1134/s1067413606050018.

Kharuk, V., Ranson, K., Oskorbin, P., Im, S., and Dvinskaya, M. (2013). Climate induced birch mortality in Trans-Baikal lake region, Siberia. *Forest Ecology and Management* 289, 385–392. DOI: 10.1016/j.foreco.2012.10.024.

Kharuk, V. I., Kuzmichev, V. V., Im, S. T., and Ranson, K. J. (2014). Birch stands growth increase in Western Siberia. *Scandinavian Journal of Forest Research* 29.5, 421–426. DOI: 10.1080/02827581.2014.912345.

Kicklighter, D. W., Cai, Y., Zhuang, Q., Parfenova, E. I., Paltsev, S., Sokolov, A. P., Melillo, J. M., Reilly, J. M., Tchebakova, N. M., and Lu, X. (2014). Potential influence of climate-induced vegetation shifts on future land use and associated land carbon fluxes in Northern Eurasia. *Environmental Research Letters* 9.3, 035004. DOI: 10.1088/1748-9326/9/3/035004.

Kreuzwieser, J. and Gessler, A. (2010). Global climate change and tree nutrition: influence of water availability. *Tree Physiology* 30.9, 1221–1234. DOI: 10.1093/treephys/tpq055.

LeBauer, D. S. and Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89.2, 371–379. DOI: 10.1890/06-2057.1.

Legout, A., K., H., Heijden, G. V. der, J-P., L., L., A., and J., R. (2014). Chemical fertility of forest soils: basic concepts. *Revue Forestière Française* SP, Fr.], ISSN 0035. DOI: 10.4267/2042/56262.

Lehmann, J. and Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*. DOI: 10.1038/nature16069.

Leppälammi-Kujansuu, J., Aro, L., Salemaa, M., Hansson, K., Kleja, D. B., and Helmisaari, H.-S. (2014). Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. *Forest Ecology and Management* 326, 79–90. DOI: 10.1016/j.foreco.2014.03.039.

Leuschner, C. and Hertel, D. (2003). Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. In: *Progress in Botany*, 405–438. DOI: 10.1007/978-3-642-55819-1_16.

Lindsay, W. L. (1979). *Chemical equilibria in soils*. John Wiley and Sons, 449 pp.

Lucht, W., Schaphoff, S., Erbrecht, T., Heyder, U., and Cramer, W. (2006). Terrestrial vegetation redistribution and carbon balance under climate change. *Carbon Balance and Management* 1.1, 6. DOI: 10.1186/1750-0680-1-6.

Lukac, M., Calfapietra, C., Lagomarsino, A., and Loreto, F. (2010). Global climate change and tree nutrition: effects of elevated CO_2 and temperature. *Tree Physiology* 30.9, 1209–1220. DOI: 10.1093/treephys/tpq040.

Malevskii-Malevich, S. P., Mol'kentin, E. K., Nadezhina, E. D., Semioshina, A. A., Sall', I. A., Khlebnikova, E. I., and Shklyarevich, O. B. (2007). Analysis of changes in fire-hazard conditions in the forests in Russia in the 20th and 21st centuries on the basis of climate modeling. *Russian Meteorology and Hydrology* 32.3, 154–161. DOI: 10.3103/s1068373907030028.

McCormack, M. L., Adams, T. S., Smithwick, E. A. H., and Eissenstat, D. M. (2014). Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95.8, 2224–2235. DOI: 10.1890/13-1942.1.

McCormack, M. L., Eissenstat, D. M., Prasad, A. M., and Smithwick, E. A. H. (2013). Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biology* 19.6, 1697–1708. DOI: 10.1111/gcb.12163.

McCormack, M. L. and Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science* 5. DOI: 10.3389/fpls.2014.00205.

McGuire, A. D., Chapin, F. S., Wirth, C., Apps, M., Bhatti, J., Callaghan, T., Christensen, T. R., Clein, J. S., Fukuda, M., Maximov, T., Onuchin, A., Shvidenko, A., and Vaganov, E. (2007). Terrestrial Ecosystems in a Changing World. In: chap. Responses of High Latitude Ecosystems to Global Change: Potential Consequences for the Climate System, 297–310. DOI: 10.1007/978-3-540-32730-1_24.

Meleshko, V. P., Kattsov, V. M., Govorkova, V. A., Sporyshev, P. V., Shkol'nik, I. M., and Shneerov, B. E. (2008). Climate of Russia in the 21st century. Part 3. Future climate changes calculated with an ensemble of coupled atmosphere-ocean general circulation CMIP3 models. *Russian Meteorology and Hydrology* 33.9, 541–552. DOI: 10.3103/s106837390809001x.

Mokhov, I. and Chernokulsky, A. (2010). Regional model assessments of forest fire risks in the Asian part of Russia under climate change. *Geography and Natural Resources* 31.2, 165–169. DOI: 10.1016/j.gnr.2010.06.012.

Monson, R. K., Lipson, D. L., Burns, S. P., Turnipseed, A. A., Delany, A. C., Williams, M. W., and Schmidt, S. K. (2006). Winter forest soil respiration controlled by climate and microbial community composition. *Nature* 439.7077, 711–714. DOI: 10.1038/nature04555.

Morel, C. and Plenchette, C. (1994). Is the isotopically exchangeable phosphate of a loamy soil the plant-available P? *Plant and Soil* 158.2, 287–297. DOI: 10.1007/bf00009502.

Muhs, D. (2007). Loess deposits, origins and properties. In: *Encyclopedia of Quaternary Science*, 1405–1418. DOI: 10.1016/b0-44-452747-8/00158-7.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., and Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386.6626, 698–702. DOI: 10.1038/386698a0.

Näsholm, T., Kielland, K., and Ganeteg, U. (2009). Uptake of organic nitrogen by plants. *New Phytologist* 182.1, 31–48. DOI: 10.1111/j.1469-8137.2008.02751.x.

Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E. (2010). CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences* 107.45, 19368–19373. DOI: 10.1073/pnas.1006463107.

Oberson, A., Friesen, D. K., Rao, I., Bühler, S., and Frossard, E. (2001). *Plant and Soil* 237.2, 197–210. DOI: 10.1023/a:1013301716913.

Oldfield, J. D. (2006). *Russian Nature: Exploring the Environmental Consequences of Societal Change*. Routledge.

Öquist, M. G., Sparrman, T., Klemedtsson, L., Harrysson Drotz, S., Grip, H., Schleucher, J., and Nilsson, M. (2009). Water availability controls microbial temperature responses in frozen soil CO_2 production. *Global Change Biology* 15.11, 2715–2722. DOI: 10.1111/j.1365-2486.2009.01898.x.

Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schafer, K. V., McCarthy, H., Hendrey, G., McNulty, S. G., and Katul, G. G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature* 411.6836, 469–472. DOI: 10.1038/35078064.

Parfitt, R. (1978). Anion adsorption by soils and soil materials. In: *Advances in Agronomy*. Vol. 30, 1–50. DOI: 10.1016/s0065-2113(08)60702-6.

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., Velde, M. van der, Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M., and Janssens, I. A. (2013). Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications* 4. DOI: 10.1038/ncomms3934.

Peñuelas, J., Sardans, J., Rivas-ubach, A., and Janssens, I. A. (2012). The human-induced imbalance between C, N and P in Earth's life system. *Global Change Biology* 18.1, 3–6. DOI: 10.1111/j.1365-2486.2011.02568.x.

Ranger, J. and Turpault, M.-P. (1999). Input–output nutrient budgets as a diagnostic tool for sustainable forest management. *Forest Ecology and Management* (122), 139–154.

Rawlins, M. A., Steele, M., Holland, M. M., Adam, J. C., Cherry, J. E., Francis, J. A., Groisman, P. Y., Hinzman, L. D., Huntington, T. G., Kane, D. L., Kimball, J. S., Kwok, R., Lammers, R. B., Lee, C. M., Lettenmaier, D. P., McDonald, K. C., Podest, E., Pundsack, J. W., Rudels, B., Serreze, M. C., Shiklomanov, A., Skagseth, Ø., Troy, T. J., Vörösmarty, C. J., Wensnahan, M., Wood, E. F., Woodgate, R., Yang, D., Zhang, K., and Zhang, T. (2010). Analysis of the Arctic System for Freshwater Cycle Intensification: Observations and Expectations. *Journal of Climate* 23.21, 5715–5737. DOI: 10.1175/2010jcli3421.1.

Reich, P. B. and Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences* 101.30, 11001–11006. DOI: 10.1073/pnas.0403588101.

Reich, P. B., Hobbie, S. E., and Lee, T. D. (2014). Plant growth enhancement by elevated CO_2 eliminated by joint water and nitrogen limitation. *Nature Geoscience* 7.12, 920–924. DOI: 10.1038/ngeo2284.

Rennenberg, H., Dannenmann, M., Gessler, A., Kreuzwieser, J., Simon, J., and Papen, H. (2009). Nitrogen balance in forest soils: nutritional limitation of plants under climate change stresses. *Plant Biology* 11, 4–23. DOI: 10.1111/j.1438-8677.2009.00241.x.

Robinson, D. A., Dewey, K. F., and Heim, R. R. (1993). Global Snow Cover Monitoring: An Update. *Bulletin of the American Meteorological Society* 74.9, 1689–1696. DOI: 10.1175/1520-0477(1993)074<1689:gscmau>2.0.co;2.

Salih, N., Ågren, G. I., and Hallbäcken, L. (2005). Modeling Response of N Addition on C and N Allocation in Scandinavian Norway Spruce Stands. *Ecosystems* 8.4, 373–381. DOI: 10.1007/s10021-003-0103-6.

Schaphoff, S., Heyder, U., Ostberg, S., Gerten, D., Heinke, J., and Lucht, W. (2013). Contribution of permafrost soils to the global carbon budget. *Environmental Research Letters* 8.1, 014026. DOI: 10.1088/1748-9326/8/1/014026.

Schaphoff, S., Reyer, C. P., Schepaschenko, D., Gerten, D., and Shvidenko, A. (2016). Tamm Review: Observed and projected climate change impacts on Russia's forests and its carbon balance. *Forest Ecology and Management* 361, 432–444. DOI: 10.1016/j.foreco.2015.11.043.

Schepaschenko, D., McCallum, I., Shvidenko, A., Fritz, S., Kraxner, F., and Obersteiner, M. (2011). A new hybrid land cover dataset for Russia: a methodology for integrating statistics,

remote sensing and in situ information. *Journal of Land Use Science* 6.4, 245–259. DOI: 10.1080/1747423x.2010.511681.

Schimel, J. P. and Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* 85.3, 591–602. DOI: 10.1890/03-8002.

Schimel, J. P., Bilbrough, C., and Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry* 36.2, 217–227. DOI: 10.1016/j.soilbio.2003.09.008.

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., and Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature* 478.7367, 49–56. DOI: 10.1038/nature10386.

Schoenholtz, S., Miegroet, H., and Burger, J. (2000). A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. *Forest Ecology and Management* 138.1-3, 335–356. DOI: 10.1016/s0378-1127(00)00423-0.

Sebestyen, S. D., Boyer, E. W., Shanley, J. B., Kendall, C., Doctor, D. H., Aiken, G. R., and Ohte, N. (2008). Sources, transformations, and hydrological processes that control stream nitrate and dissolved organic matter concentrations during snowmelt in an upland forest. *Water Resources Research* 44.12. DOI: 10.1029/2008wr006983.

Shibata, H., Hasegawa, Y., Watanabe, T., and Fukuzawa, K. (2013). Impact of snowpack decrease on net nitrogen mineralization and nitrification in forest soil of northern Japan. *Biogeochemistry* 116.1-3, 69–82. DOI: 10.1007/s10533-013-9882-9.

Shkol'nik, I. M., Mol'kentin, E. K., Nadezhina, E. D., Khlebnikova, E. I., and Sall, I. A. (2008). Temperature extremes and wildfires in Siberia in the 21st century: the MGO regional climate model simulation. *Russian Meteorology and Hydrology* 33.3, 135–142. DOI: 10.3103/s1068373908030011.

Shuman, J. K., Tchebakova, N. M., Parfenova, E. I., Soja, A. J., Shugart, H. H., Ershov, D., and Holcomb, K. (2015). Forest forecasting with vegetation models across Russia. *Canadian Journal of Forest Research* 45.2, 175–184. DOI: 10.1139/cjfr-2014-0138.

Shvidenko, A. Z., Gustafson, E., McGuire, A. D., Kharuk, V. I., Schepaschenko, D. G., Shugart, H. H., Tchebakova, N. M., Vygodskaya, N. N., Onuchin, A. A., Hayes, D. J., McCallum, I., Maksyutov, S., Mukhortova, L. V., Soja, A. J., Belelli-Marchesini, L., Kurbatova, J. A., Oltchev, A. V., Parfenova, E. I., and Shuman, J. K. (2012). Terrestrial Ecosystems and Their Change. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 6, 171–249. DOI: 10.1007/978-94-007-4569-8_6.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S., and Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56.3–4, 274–296. DOI: 10.1016/j.gloplacha.2006.07.028.

Stireman, J. O., Dyer, L. A., Janzen, D. H., Singer, M. S., Lill, J. T., Marquis, R. J., Ricklefs, R. E., Gentry, G. L., Hallwachs, W., Coley, P. D., Barone, J. A., Greeney, H. F., Connahs, H., Barbosa, P., Morais, H. C., and Diniz, I. R. (2005). Climatic unpredictability and parasitism of caterpillars: Implications of global warming. *Proceedings of the National Academy of Sciences* 102.48, 17384–17387. DOI: 10.1073/pnas.0508839102.

Takala, M., Pulliainen, J., Metsamaki, S., and Koskinen, J. (2009). Detection of Snowmelt Using Spaceborne Microwave Radiometer Data in Eurasia From 1979 to 2007. *IEEE Trans. Geosci. Remote Sensing* 47.9, 2996–3007. DOI: 10.1109/tgrs.2009.2018442.

Tchebakova, N. M., Parfenova, E. I., Lysanova, G. I., and Soja, A. J. (2011). Agroclimatic potential across central Siberia in an altered twenty-first century. *Environmental Research Letters* 6.4, 045207. DOI: 10.1088/1748-9326/6/4/045207.

Tchebakova, N. M., Parfenova, E., and Soja, A. J. (2009). The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4.4, 045013. DOI: 10.1088/1748-9326/4/4/045013.

Tchebakova, N. M., Rehfeldt, G. E., and Parfenova, E. I. (2010). From vegetation zones to climatypes: Effects of climate warming on Siberian ecosystems. In: *Permafrost Ecosystems. Siberian Larch Forests*. Chap. 22, 427–447.

van Groenigen, K.-J., Six, J., Hungate, B. A., de Graaff, M.-A., van Breemen, N., and van Kessel, C. (2006). Element interactions limit soil carbon storage. *Proceedings of the National Academy of Sciences* 103.17, 6571–6574. DOI: 10.1073/pnas.0509038103.

Vitousek, P. M., Porder, S., Houlton, B. Z., and Chadwick, O. A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications* 20.1, 5–15. DOI: 10.1890/08-0127.1.

von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., and Flessa, H. (2006). Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *European Journal of Soil Science* 57.4, 426–445. DOI: 10.1111/j.1365-2389.2006.00809.x.

Walker, T. and Syers, J. (1976). The fate of phosphorus during pedogenesis. *Geoderma* 15.1, 1–19. DOI: 10.1016/0016-7061(76)90066-5.

Wardle, D. A. (2004). Ecological Linkages Between Aboveground and Belowground Biota. *Science* 304.5677, 1629–1633. DOI: 10.1126/science.1094875.

Wieder, W. R., Cleveland, C. C., Lawrence, D. M., and Bonan, G. B. (2015). Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study. *Environmental Research Letters* 10.4, 044016. DOI: 10.1088/1748-9326/10/4/044016.

Yano, Y., Brookshire, E. N. J., Holsinger, J., and Weaver, T. (2015). Long-term snowpack manipulation promotes large loss of bioavailable nitrogen and phosphorus in a subalpine grassland. *Biogeochemistry* 124.1-3, 319–333. DOI: 10.1007/s10533-015-0100-9.

Yuan, Z. Y. and Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. *Critical Reviews in Plant Sciences* 29.4, 204–221. DOI: 10.1080/07352689.2010.483579.

Yuan, Z. Y. and Chen, H. Y. H. (2012a). A global analysis of fine root production as affected by soil nitrogen and phosphorus. *Proceedings of the Royal Society B: Biological Sciences* 279.1743, 3796–3802. DOI: 10.1098/rspb.2012.0955.

Yuan, Z. Y. and Chen, H. Y. H. (2012b). Fine root dynamics with stand development in the boreal forest. *Functional Ecology* 26.4, 991–998. DOI: 10.1111/j.1365-2435.2012.02007.x.

Zhang, T. (2005). Influence of the seasonal snow cover on the ground thermal regime: An overview. *Reviews of Geophysics* 43.4. DOI: 10.1029/2004rg000157.

Chapter 2

Site selection and characteristics

We selected six sites in SW Siberia with contrasting climate and soil conditions (Fig. 2.1 and Tables 2.1 and 2.2). These sites were positioned in the forest-steppe and sub-taiga bioclimatic zones. Their common characteristics were a soil developed on loess parent material and a similar vegetation cover in terms of dominant species. Each site presented aspen (*Populus tremula* L.) stands with closed canopy along with nearby grassland areas. Study areas were set up in each of these vegetation covers. One site (SAW) only had forest cover with aspen. So there were six sites with forest and five with grassland in our data set for SW Siberia.

Climate change trends are shown in Fig. 2.2–2.4.

From their common origin as loess deposits, soil have undergone different forming processes due to the action of climate and vegetation. The pedological horizons described in the study sites are shown in Fig. 2.5. The main physico-chemical properties of soils are given in the Table 2.3 and Fig. 2.6 and 2.7.

There were three groups of sites corresponding to different intensity of investigation, as described in Fig. 2.8.

Selection criteria and descriptive informations of our study sites are reminded in each chapter, as well as additional specific details.

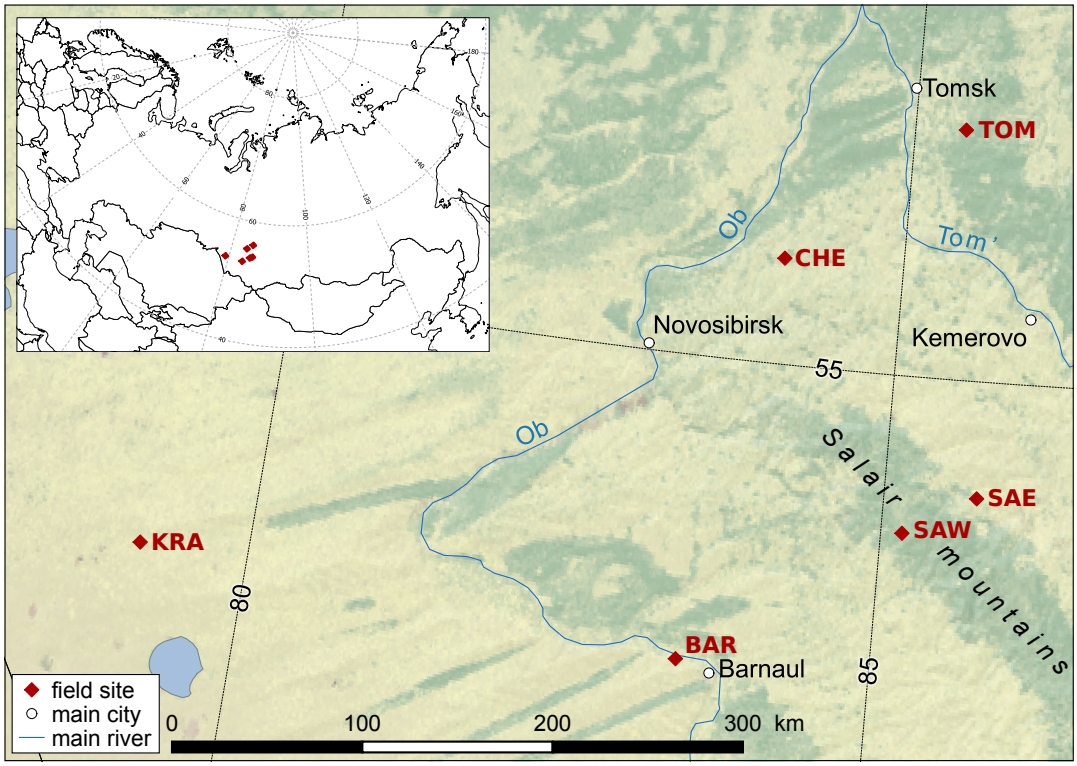


Figure 2.1: Location of the study sites in SW Siberia. The names of the field sites are based on the name of the closest city or of the geographical area: Barnaul (BAR), Chebula (CHE), Krasnozerskoye (KRA), Salair East (SAE), Salair West (SAW), and Tomsk (TOM).

Table 2.1: Main characteristics of the study sites.

Site ID	BAR	CHE	KRA	SAE	SAW	TOM
Geographical characteristics						
Name[a]	Barnaul	Chebula	Krasnozerskoye	Salair East	Salair West	Tomsk
Ecological zone	Forest-steppe (southern part)	Forest-steppe (northern part)	Steppe to Forest-steppe	Sub-taiga to Forest-steppe	"Blackish taiga"	Sub-taiga
Latitude (°N)	53.41	55.55	53.59	54.39	54.18	56.30
Longitude (°E)	83.47	84.00	79.14	85.75	85.17	85.43
Elevation (m asl)	221	186	141	305	358	232
Soil classification						
Soil in forest	Haplic Phaeozem	Haplic Phaeozem	Phaeozem	Leptic Phaeozem	Haplic Luvisol	Albic Luvisol
Soil in grassland	Calcic Chernozem	Haplic Phaeozem	Calcic Hortic Chernozem	Leptic Phaeozem		Albic Luvisol
Forest stand characteristics (mean values)						
Density (tree ha^{-1})	1664	387	767	1883	1144	1139
DBH[b] (cm)	14.9	33.9	26.3	13.7	22.8	21.4
Height (m)	11.2	28.0	18.7	15.7	24.8	18.2
Age (years)	27	62	51	21	47	56

[a]name of the closest city or name of the local area; [b]diameter at breast height (1.3 m)

Table 2.2: Detailed climatic features of the study sites. Data averaged on the period 1981–2010. The data presented for each site come from the closest weather stations.

Variable	Period	BAR	CHE	KRA	SAE	SAW	TOM
WMO index of the station		29838	29539	29915	29745	29736	29430
Distance site–station (km)		4	28	76	18	64	38
Air Temperature (°C)	MAT	2.7	1.3	2.9	2.3	1.2	0.9
	DJF	-14.1	-15.2	-15.1	-15.4	-17.6	-15.6
	MAM	3.4	2.0	3.4	3.4	2.8	1.6
	JJA	18.3	17.0	19.7	17.4	16.9	16.7
	SON	2.8	1.2	3.2	3.0	2.2	0.8
Precipitation (mm)	MAP	431.5	509.8	324.5	432.3	453.0	566.5
	DJF	69.8	84.5	53.2	54.3	66.1	104.7
	MAM	85.1	91.3	58.2	78.9	75.1	98.2
	JJA	166.6	184.8	135.3	182.2	168.8	202.9
	SON	107.7	146.4	76.1	106.1	115.9	157.2
Snow Height (cm)	climax	48.8	42.5	18.8	38.0	54.3	70.6
SCD 1 cm (days)	year	157.2	167.6	141.9	144.5	149.5	178.1
SCD 20 cm (days)	year	108.3	118.3	25.2	88.3	116.4	145.5
Soil Temp. at 20 cm (°C)	DJF	-1.5		-6.0			-0.4
	MAM	4.3		4.0			2.4
	JJA	18.9		20.3			16.4
	SON	6.5		7.3			5.8
Soil frozen at 20 cm (days)	year	86.8		130.1			44.5
Depth of soil frozen (m)	DJF	20–40		40–80			0–20

WMO: World Meteorological Organization; MAT: mean annual temperature;
MAP: mean annual precipitations; SCD: snow cover duration;
D, J, F, M, A, M, J, J, A, S, O and N are the months of the year
climax: maximum snow depth, i.e. mean between mid-February and mid-March

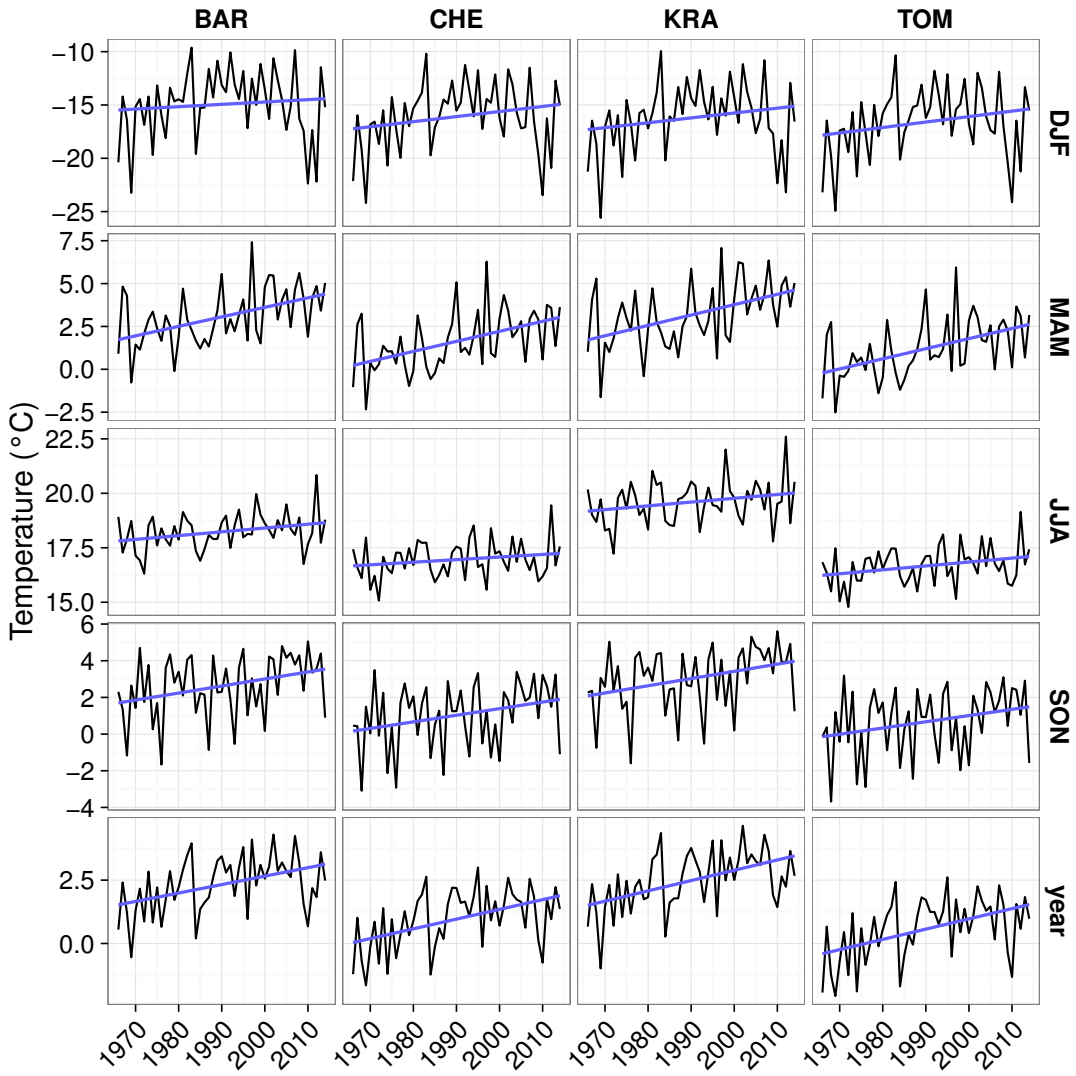


Figure 2.2: Seasonally and yearly averaged daily mean air temperature on four of our study sites over the period 1966–2014. The blue lines are simple linear regressions. J, F, M, A, M, J, J, A, S, O, N, and D are the months of the year.

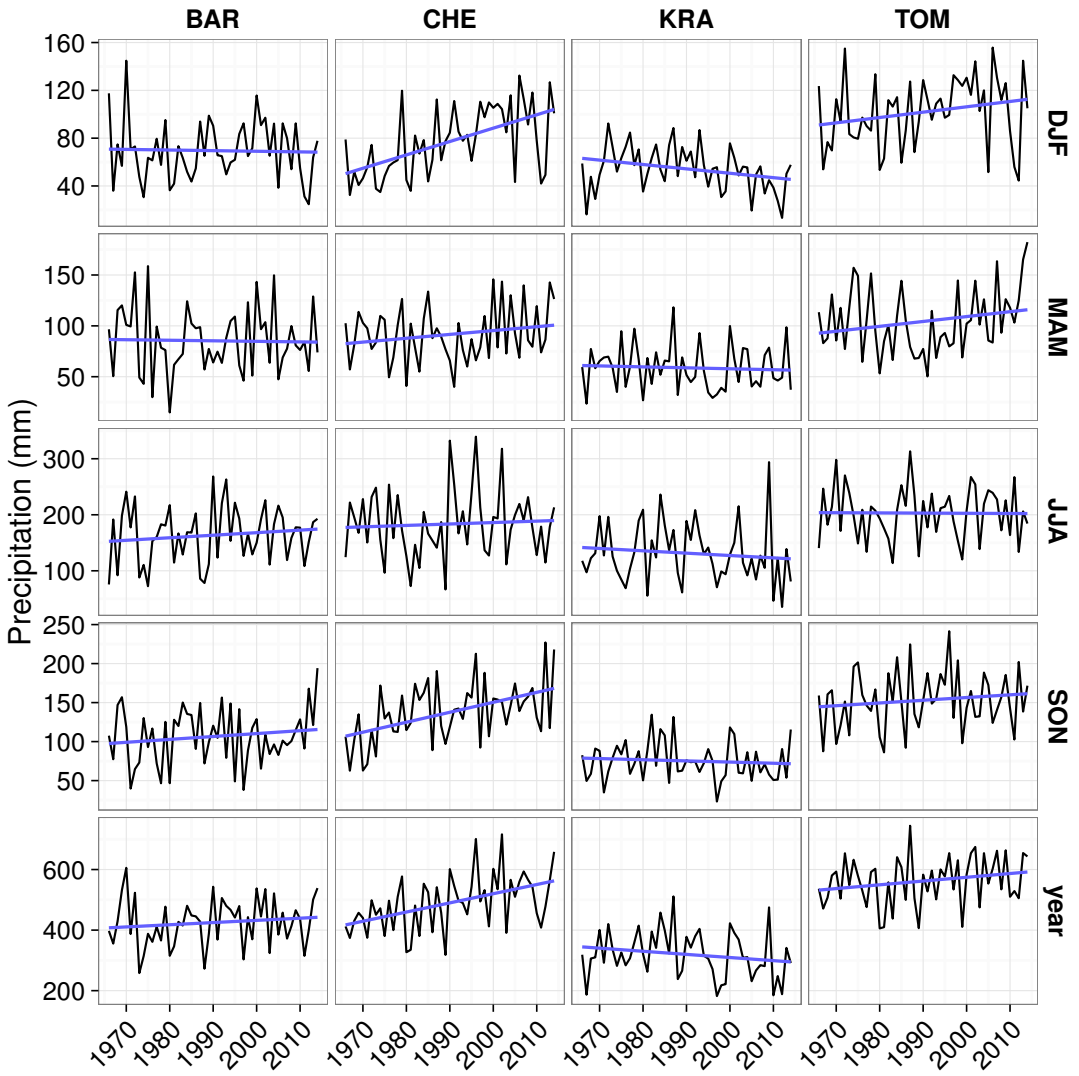


Figure 2.3: Seasonally and yearly summed precipitations on four of our study sites over the period 1966–2014. The blue lines are simple linear regressions. J, F, M, A, M, J, J, A, S, O, N, and D are the months of the year.

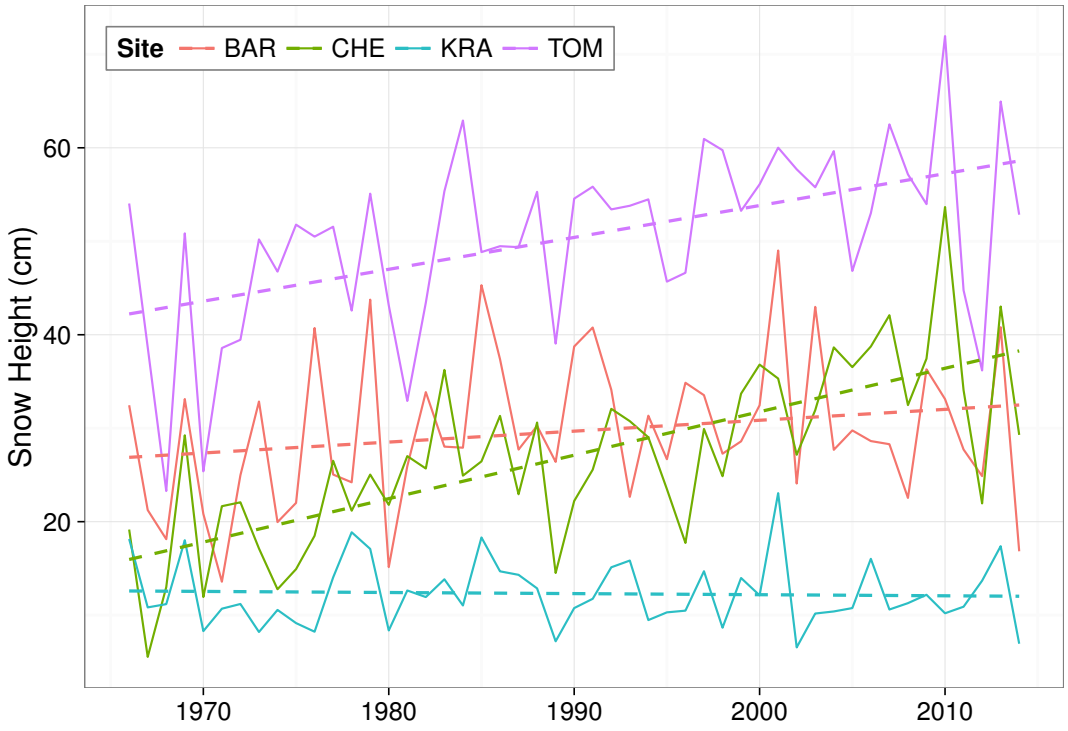


Figure 2.4: Annual mean snow height averaged between December and April over the period 1966–2014. The dashed lines are simple linear regressions.

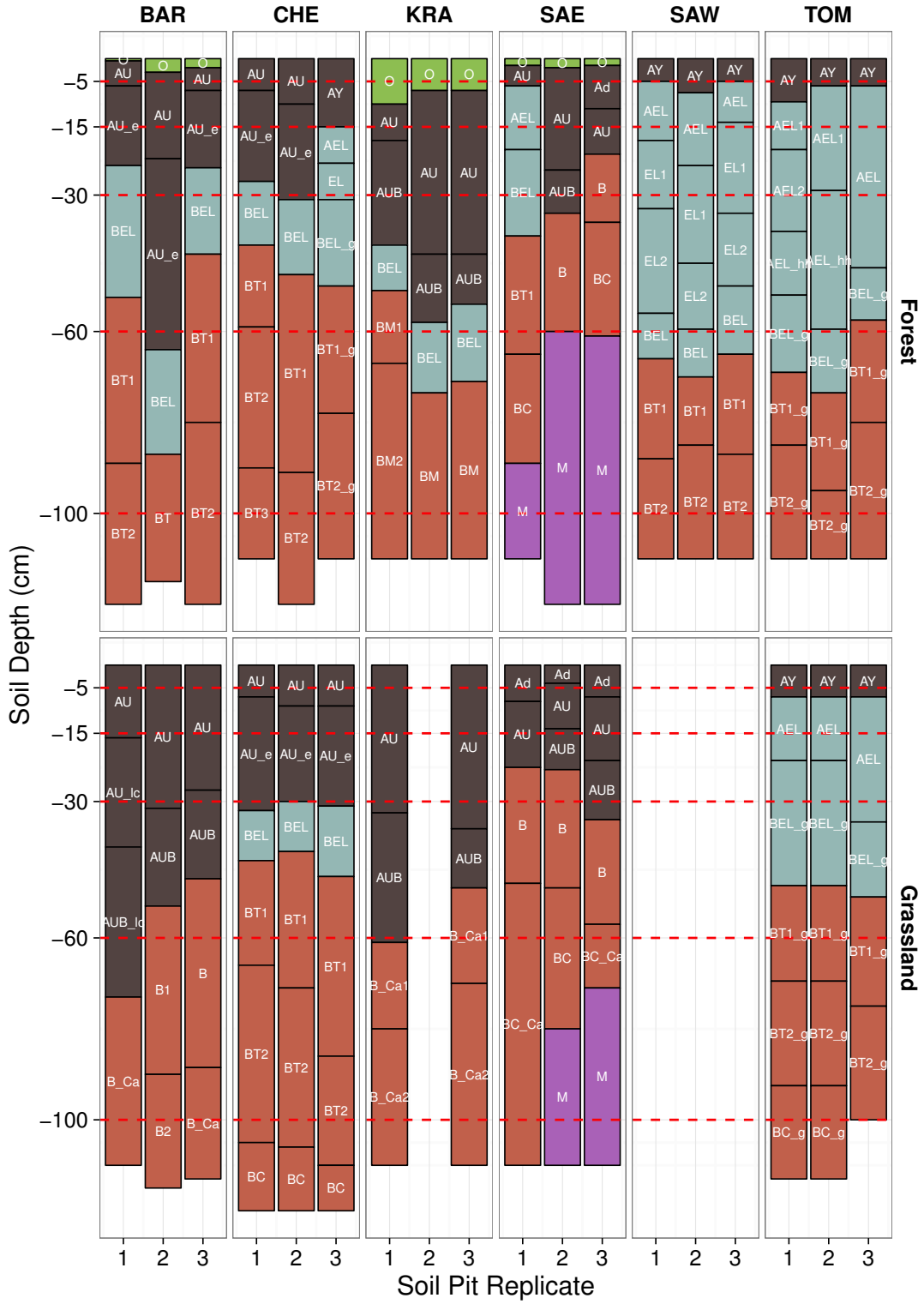


Figure 2.5: Description of the soil horizons observed in three pit replicates at our study sites under aspen forest and grassland vegetation covers.

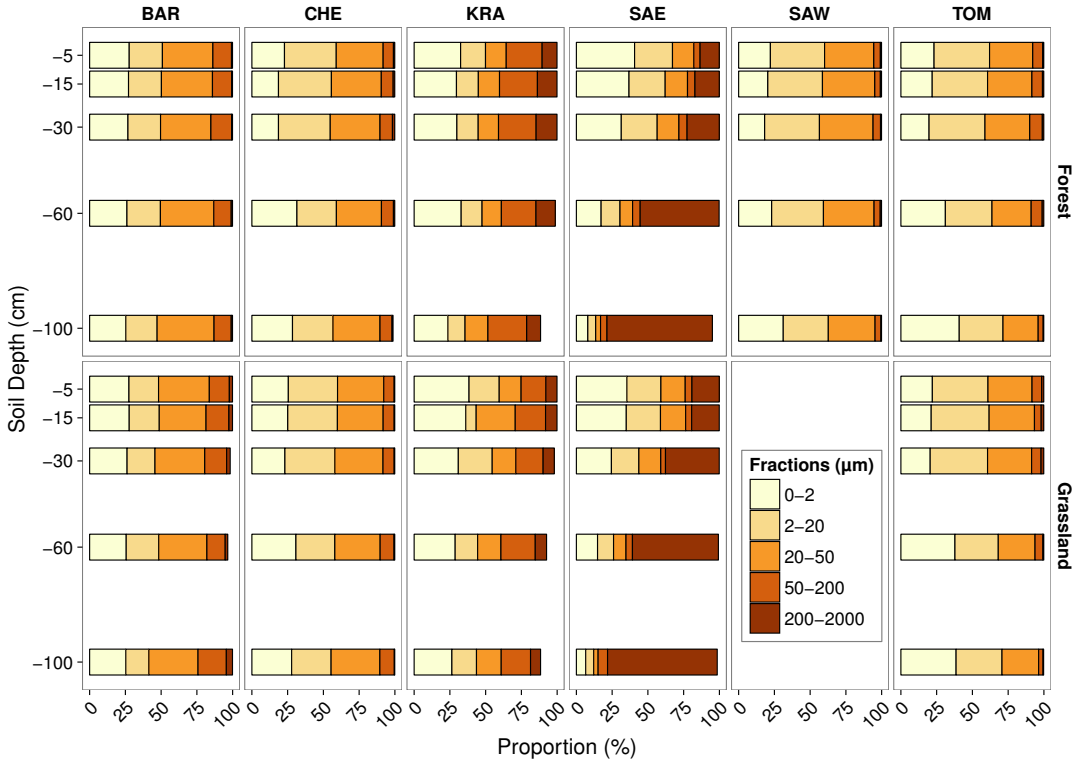


Figure 2.6: Soil granulometry throughout a 1 m depth profile. Measurements on composite samples made from 3 soil pits per site.

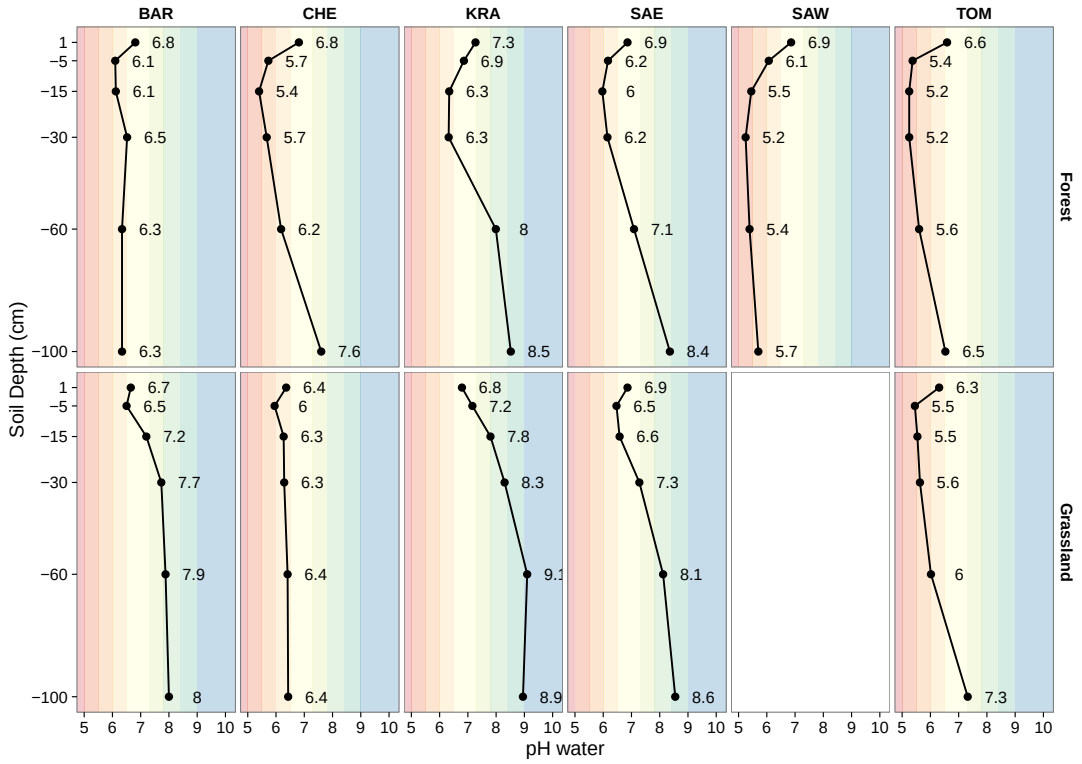


Figure 2.7: Profiles of soil and litter pH–H_2O. Measurements on composite samples made from 3 soil pits per site. "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands) that is to say mainly OL and OF horizons, and eventually OH (at BAR, CHE, KRA and SAE) at the date of sampling (July 2013).

Table 2.3: Main soil physico-chemical properties.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
Apparent density											
−5	1.0	0.8	0.7	0.5	0.7	0.9	1.0	1.0	0.9	0.9	0.9
−15	1.2	1.0	1.0	0.8	1.0	1.1	1.3	1.1	1.0	1.1	1.2
−30	1.2	1.2	1.2	1.1	1.3	1.2	1.3	1.1	1.2	1.3	1.3
−60	1.3	1.4	1.4	1.3	1.5	1.5	1.7	1.4	1.4	1.3	1.5
−100	1.4	1.5	1.6	1.1	1.6	1.4	1.7	1.4	1.5	1.4	1.4
Organic C ($g\,kg^{-1}$)											
−5	39.20	53.00	54.30	113.00	52.90	37.20	35.30	40.30	68.10	51.20	32.50
−15	32.80	22.40	34.90	63.60	25.00	24.80	29.10	35.40	42.80	46.10	21.30
−30	28.60	10.70	25.00	16.90	13.10	13.90	18.20	28.50	30.80	6.79	10.70
−60	8.05	3.68	6.79	3.07	4.92	5.49	5.71	4.35	12.80	2.86	3.76
−100	2.73	2.43	3.68	1.26	2.43	2.99	2.79	2.68	3.07	1.11	2.33
Total N ($g\,kg^{-1}$)											
−5	2.91	3.48	4.10	8.53	4.22	2.92	2.83	2.80	5.32	3.90	2.65
−15	2.44	1.47	2.57	4.65	2.14	2.09	2.31	2.40	3.23	3.47	1.77
−30	2.09	0.75	1.85	1.21	1.15	1.17	1.45	1.89	2.34	0.48	0.85
−60	0.65	0.36	0.58	0.26	0.45	0.50	0.51	0.38	1.01	0.22	0.40
−100	0.26	0.25	0.31	0.09	0.29	0.36	0.21	0.27	0.24	0.10	0.29
Total P ($g\,kg^{-1}$)											
−5	1.02	0.85	0.73	1.10	1.04	0.76	0.88	0.96	0.85	0.92	0.69
−15	0.95	0.66	0.62	0.91	0.86	0.68	0.86	0.94	0.70	0.87	0.62
−30	0.96	0.63	0.54	0.42	0.77	0.56	0.76	0.90	0.63	0.56	0.53
−60	0.76	0.68	0.39	0.32	0.59	0.49	0.59	0.69	0.52	0.61	0.49
−100	0.64	0.66	0.41	0.32	0.65	0.53	0.59	0.69	0.41	0.59	0.54

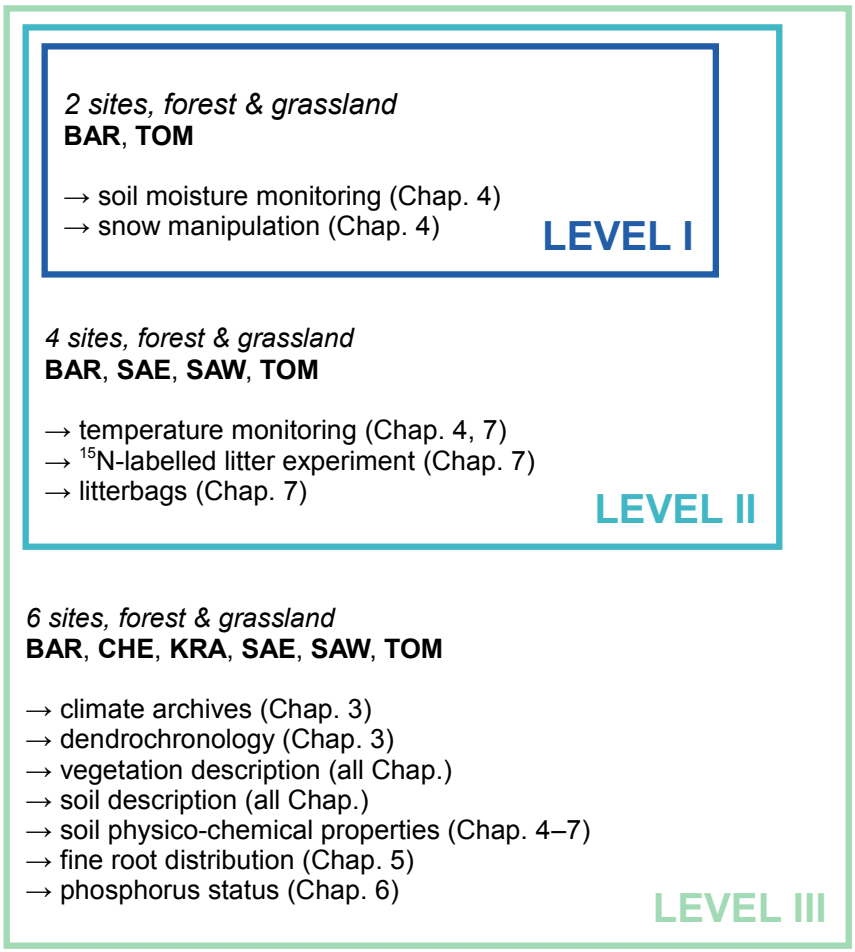


Figure 2.8: Investigation levels at our study sites in SW Siberia. Field site names, based on the name of the closest city or of the geographical area: Barnaul (BAR), Chebula (CHE), Krasnozerskoye (KRA), Salair East (SAE), Salair West (SAW), and Tomsk (TOM).

Chapter 3

A latitudinal response of aspen growth to climate along a pedoclimatic gradient in south-western Siberia

In collaboration with: J.-L. Dupouey, M. R. Bakker, P. A. Barsukov, D. Derrien, Z. E. Kayler, A. Legout, P. Nikitich, O. Rusalimova, and B. Zeller.

3.1 Introduction

To understand the responses of terrestrial ecosystems to the variation in their environmental conditions is of primary importance in order to predict the ecological impacts of global change. In particular, knowledge on tree growth control by environmental factors is needed to predict the evolution of forest productivity, community composition and biogeography under future conditions.

Northern Eurasia experiences a particularly strong intensity of global change (IPCC 2013). As such, substantial reshaping of ecosystems is expected (Groisman and Gutman 2012). Longer vegetation growing seasons and frost-free periods, melt of permafrost in northern areas and modification of soil freeze–thaw cycles in southern areas are projected with the rising of average air temperature (Groisman et al. 2012). Probable changes in the intensity and the distribution of precipitations could modify fire and hydrological regimes (Shiklomanov and Lammers 2009; Shkolnik et al. 2010; Soja et al. 2007). Covering about 10 million km^2, Siberia occupies a great part of Northern Eurasia. Along with the wide latitudinal gradient Siberia covers (from 45 to 75 °N of latitude), several bioclimatic zones have been identified, from south to north: steppe, forest-steppe, sub-taiga, southern taiga, middle taiga, northern taiga, forest tundra and tundra. As a consequence of altered physical conditions, the composition of the vegetation communities may change, as well as the positions and the areas of the bioclimatic zones. In particular, all bioclimatic zones have been predicted to shift northwards, steppe and forest-steppe to spread over larger areas at the expense of taiga zones while tundra ecosystems may be constrained to small local areas in the Arctic polar circle (Jiang et al. 2012; Shuman et al. 2015; Soja et al. 2007; Tchebakova et al. 2009, 2010). While primary productivity may be enhanced

by higher air temperatures and CO_2 concentrations (Mooney et al. 1991; Morgan et al. 2004; Norby et al. 2005; Schimel 1995) along with longer vegetation growing seasons, water shortages might appear with drier summer conditions, particularly in the southern part of Siberia (Alcamo et al. 2007; Tchebakova et al. 2011a,b). Even though there is an increasing interest in the study of Siberian ecosystems, functional ecological data remain sparse in the international literature (Gordov and Vaganov 2010; Groisman and Soja 2009). In particular, few data have been published on fine regional scales.

In this study we were interested in south-western (SW) Siberia, which is located on the transition between steppe and southern-taiga. The south of Siberia has historically been more populated than the rest of Siberia and the south-west concentrates the highest population density because climatic conditions allow agriculture. This region is characterized by a cold-temperate climate with cold winters and temperate summers. Daily mean temperature ranges between −17 °C (January) and 19 °C (July), with extremes of −45 °C and 30 °C. Annual mean precipitation ranges from about 300 mm in the south (steppe) to 600 mm in the north (southern-taiga). Winter is characterized by a seasonally permanent snow cover lasting several months. Both snow-pack duration and snow height increase on a gradient towards the north. Along with this climate gradient, SW Siberia is positioned on a gradient of soil-forming processes. In the south, typically in the forest-steppe zone, the main soil-forming processes are the formation and accumulation of organic matter, leaching of carbonates in the topsoil and formation of secondary carbonates in deep soil layers. Soils belong to the groups of Chernozems and Phaeozems (Jones et al. 2009). In the north, typically in southern and sub-taiga, there are no Chernozems, Phaeozems are less frequent and Luvisols appear. The main soil-forming processes are related to the periodical movements of the water table, clays are washed from the topsoil and accumulate in the deeper layers and carbonates have disappeared from the first metre of the soil profile. Biogeochemical processes probably vary in nature and kinetics along the pedoclimatic gradient, as reflected notably by litter decomposition which is faster in sub-taiga than in forest-steppe (Chap. 7).

Soil and vegetation processes are tightly coupled through numerous feedbacks, and both are controlled by climate. The climate control on vegetation growth can be direct—e.g. through the effects of climate on plant physiology and/or phenology (Wipf and Rixen 2010)—and/or indirect—e.g. through the effects of climate on microbial and biogeochemical processes controlling water and nutrient availability (Brooks et al. 2011; van der Heijden et al. 2008). In SW Siberia, it can be expected that winter processes, in relation to snow features such as height of the snow-pack and duration of the snow season (Chap. 4), exert significant controls on biogeochemical processes and biological activity. In fact, snow-packs have thermal insulating properties and control soil temperature at wintertime (Brooks et al. 2011; Zhang 2005). In SW Siberia, soils do not freeze in the northern zone (southern and

sub-taiga), where the snow height is the highest, while in the southern part (steppe and forest-steppe) soil freezing occurs in winter, depending on the soil status at the date of the seasonal snow-pack installation and on its height (Chap. 4). Such differences on winter soil temperature are known to impact microbial activity and, by extension, biogeochemical processes and the release of plant-available nutrients (Brooks et al. 2011; Schimel et al. 2004). The amount of snow also controls the amount of water released at snow-melt (Brooks et al. 2011; Hardy et al. 2001; Iwata et al. 2010). In SW Siberia, the snow-melt constitutes the major input of water in the year (Chap. 4). While the soil water reserve is almost always filled at snow-melt in the northern part of SW Siberia, in the south the level of its recharge depends on both the water budget in the previous summer and on the amount of snow (Chap. 4). With climate change, an increase of the accumulation of snow has been observed and is projected for the next decades in SW Siberia (Bulygina et al. 2011, 2010, 2009; Groisman et al. 2006; Shkolnik et al. 2010). Changes in snow regime are known to have diverging effects on vegetation productivity (Brooks et al. 2011; Wipf and Rixen 2010). For example, in Central Siberia, higher plant productivity was observed after deep snow-pack and delayed snow-melt, possibly because of soil thermal insulation and/or increased water availability (Grippa et al. 2005). On the contrary, in sub-Arctic Eurasia, delayed snow-melt due to higher snow-pack impacted cambial activity initiation and reduced tree-growth sensitivity to summer temperature, possibly participating in a decrease of productivity (Kirdyanov et al. 2003; Vaganov et al. 1999). Furthermore, since the soil moisture content during the growing season interacts with microbial and vegetation activities, snow exerts indirect control on summer processes in regions with low summer precipitations and where the soil moisture content depends on the input of melt-water (Chimner and Welker 2005; Walker et al. 1999).

Aspen (*Populus tremula* L.) and birch (*Betula pendula* Roth.) are two common tree species commonly found in SW Siberia, particularly in the forest-steppe zone (Schepaschenko et al. 2011). If aspen and birch currently occupy about 12 % of the total forested area of Siberia and Russian Far East (Shepashenko et al. 1998), some bioclimatic models project a significant increase of the area they occupy at the end of the 21st century (Shuman et al. 2015). Even outside of Siberia, literature on aspen and birch growth control in natural ecosystems remain sparse. Trembling aspens—the Eurasian species *Populus tremula* L. (European Common Aspen) and its North American relative *Populus tremuloides* Michx. (American Quaking Aspen)—are among the most widespread woody species in the world (Dickmann and Kuzovkina 2008; Húlten and Fries 1986). These two species are close (Cervera et al. 2005; Eckenwalder 1996; Müller et al. 2012; Pakull et al. 2009), they grow under similar climatic conditions in Europe and North America and are adapted to harsh environments. European aspen generally grows in small stands (0.1–2 ha) most of which consist of a single clone regenerated by suckering while quaking aspen usually grows in larger stands (a clone

of 43.3 ha has been reported) (Kemperman and Barnes 1976). Aspen species play a significant ecological role in boreal forest structure and function (Kouki et al. 2004; Suominen et al. 2003), have an increasing value in the traditional forest industry (Johansson 1996), and may be utilized for bio-energy production (Johansson 2002; Karacic and Weih 2006), or even for phyto-remediation (Laureysens et al. 2005). Due to their large genotypic and phenotypic variabilities, aspen species may achieve a relatively high adaptability to future climatic conditions (Hajek et al. 2013; Hamrick 2004; Ingvarsson 2005; Jansson and Douglas 2007; Soolanayakanahally et al. 2015; Yin et al. 2008). The North-American aspen has been more studied than the Eurasian one. In particular, *P. tremuloides* site productivity was shown to depend mainly on soil nutrient and moisture regimes (Chen et al. 1998, 2002; Hogg et al. 2013; Huang et al. 2010; Leonelli et al. 2008; Messaoud and Chen 2011). Other local environmental factors, influencing tree functioning and health, also impact quaking aspen growth, such as insect outbreaks (Hogg et al. 2002; Hogg 1999), root diseases (Brandt et al. 2003), light availability (Hemming and Lindroth 1999) or soil temperature (Peng and Dang 2003). *P. tremuloides* is sensitive to severe and prolonged warm droughts (Hanna and Kulakowski 2012; Michaelian et al. 2011; Worrall et al. 2010).

In this study, we aimed at characterizing the main drivers of *P. tremula* growth in SW Siberia. We hypothesized that both the average growth levels and the response to the year-to-year climate variability vary along with the gradient of pedoclimatic conditions. In particular, it is unclear whether the higher temperatures and the longer growing seasons in the south enhance tree growth or if the latter is limited by drier summer conditions, in comparison with the colder but moister conditions of the north of SW Siberia. Also, we hypothesized that tree growth responds to soil water availability and to snow cover level—since it is an important control of the soil moisture content during the growing vegetation season—in the steppe–forest-steppe zone (the south of SW Siberia) while it responds to early spring and summer temperature—which control the length of the growing season and the amount of energy available for carbon assimilation—in sub-taiga (north). Finally, it is possible that productivity was modified in the recent decades if global change alleviated or exacerbated, or started to do so, growth limitations in SW Siberia. To test our hypotheses, we measured tree-ring width in 21 aspen stands of diverging age in six sites distributed on the transition between steppe and sub-taiga in SW Siberia. Mean ring-widths were compared between sites and between periods of growth in the last century. Local standard chronologies were related to a selection of climate (air temperature, precipitation, snow height), or climate-related (soil temperature, soil water content and tree water stress index), parameters following bootstrapped correlation/response functions procedures on monthly and 15 days time steps. We discussed how the climate (-related) variables significantly correlated to stem radial growth are susceptible to control either directly, through plant physiology and phenology, or indirectly, through microbial and biogeochemical processes related to

Table 3.1: Main characteristics of the study sites.

Site ID	Name[a]	Bioclimatic zone	Lat. N	Long. E	Elev.[b]	Soil[c]
BAR	Barnaul	Forest-steppe (southern part)	53.41	83.47	221	Haplic Phaeozem
CHE	Chebula	Forest-steppe (northern part)	55.55	84.00	186	Haplic Phaeozem
KRA	Krasno-zerskoye	Steppe to forest-steppe	53.59	79.14	141	Phaeozem
SAE	Salair East	Sub-taiga to forest-steppe	54.39	85.75	305	Leptic Phaeozem
SAW	Salair West	"Blackish taiga"	54.18	85.17	358	Haplic Luvisol
TOM	Tomsk	Sub-taiga	56.30	85.43	232	Albic Luvisol

[a]name of the closest city or name of the local area; [b]elevation (m above sea level)
[c]WRB classification (IUSS Working Group WRB 2014)

water and nutrient plant-availability, tree growth in the region. Finally, we initiated a reflection on the potential implications of our findings in the context of global change.

3.2 Materials and methods

3.2.1 Site description

We selected six sites in SW Siberia located on the transition from steppe to sub-taiga and with contrasting pedoclimatic conditions (Table 3.1). Krasnozerskoye (hereafter noted KRA) is located on the border of steppe and forest-steppe, Barnaul (BAR) in the southern part of forest-steppe, Chebula (CHE) in the northern part of forest-steppe, Salair East (SAE) on the transition between sub-taiga and forest-steppe in the foothills of the Salair mountains range, Salair West (SAW) in the "Blackish" taiga belt of Salair mountains, and Tomsk (TOM) in sub-taiga. Sites located in the forest-steppe are expected to be drier, to have higher mean temperature and to experience a lower height of snow during winter than sites located in the sub-taiga. The same phenomenon is expected from the South to the North, with the exception of SAW which is located in a low-mountain range and experiences climatic conditions similar to TOM, our northernmost site. Detailed climate characteristics are provided in Table 3.2.

At all the six study sites, the soil has developed on loess parent material. Over our gradient of climatic conditions, the soils present a rather homogeneous nutrient status but somehow diverging soil-forming processes led to differences in soil

Table 3.2: Detailed climatic features of the study sites. Data averaged on the period 1981–2010. The data presented for each site come from the closest weather station(s).

Variable	Period	BAR	CHE	KRA	SAE	SAW	TOM
WMO index of the station		29838	29539	29915	29745	29736	29430
Distance site–station (km)		4	28	76	18	64	38
Air Temperature (°C)	MAT	2.7	1.3	2.9	2.3	1.2	0.9
	DJF	-14.1	-15.2	-15.1	-15.4	-17.6	-15.6
	MAM	3.4	2.0	3.4	3.4	2.8	1.6
	JJA	18.3	17.0	19.7	17.4	16.9	16.7
	SON	2.8	1.2	3.2	3.0	2.2	0.8
Precipitation (mm)	MAP	431.5	509.8	324.5	432.3	453.0	566.5
	DJF	69.8	84.5	53.2	54.3	66.1	104.7
	MAM	85.1	91.3	58.2	78.9	75.1	98.2
	JJA	166.6	184.8	135.3	182.2	168.8	202.9
	SON	107.7	146.4	76.1	106.1	115.9	157.2
Snow Height (cm)	climax*	48.8	42.5	18.8	38.0	54.3	70.6
Snow Cover Duration 1 cm (days)	year	157.2	167.6	141.9	144.5	149.5	178.1
Snow Cover Duration 20 cm (days)	year	108.3	118.3	25.2	88.3	116.4	145.5
Soil Temperature at −20 cm (°C)	DJF	-1.5		-6.0			-0.4
	MAM	4.3		4.0			2.4
	JJA	18.9		20.3			16.4
	SON	6.5		7.3			5.8
Nb of days with soil frozen at −20 cm	year	86.8		130.1			44.5
Average depth of soil frozen (m)	DJF	20–40		40–80			0–20

WMO: World Meteorological Organization; MAT: mean annual temperature; MAP: mean annual precipitations; D, J, F, M, A, M, J, J, A, S, O and N are the months of the year

*climax: maximum snow cover depth, mean snow depth between mid-February and mid-March

physico-chemical conditions. Notably, pH varies between sites (5.25–6.86 in the 15 first cm and 5.70–8.52 at −100 cm), SAW and TOM (the two sites in sub-taiga) present a periodically high water table and one site (SAE) presents a thinner loess layer (about 80 cm laying on the top of a fractionated schist material while at all the other sites the bedrock cannot be reached in the first 120 cm). Fine root (< 0.8 mm diameter) exploration occurs deeper in forest-steppe than in sub-taiga (Chap. 5, Brédoire et al. 2016b).

At each site, we selected 3–4 forest stands dominated by aspen (*Populus tremula* L.; Table 3.3). These three stands were spaced by 200–2000 m and were defined as containing at least 30 aspen trees. We selected on each site one stand with diverging age (younger or older than the other two/three stands, which were more representative for the site). All trees and shrub species were identified and individual stems counted. We measured the circumference at 1.30 m of all trees, the height of at least 10 aspen trees per stand using a clinometer (Suunto Optical Reading Clinometer PM-5/400 PC) and assessed diameter and estimated height of all shrubs taller than 1.30 m. Leaf area index (LAI) was estimated by collecting litterfall in autumn 2013. Five littertraps of 1.96 m^2 each were installed out earlier in the season on each site. We sorted the litterfall to keep only the leaves and oven dried them at 60 °C to constant weight. For each site, the surface area and the dry weight of 20 leaves was then used to compute LAI in m^2 leaves m^{-2} ground.

Understorey vegetation cover (woody and herbaceous) was described on an area of 100 m^2 in each study stand. All species were identified and their percent coverage was visually estimated based on the Braun-Blanquet scale (Braun-Blanquet et al. 1932) consisting of a plus sign (sparse and covering a small area) and a series of numbers from 1 to 5 (5 is covering more than 75 % of the area). For each site and each species, we calculated the mean score on the Braun-Blanquet scale (ignoring the "+" class) and assumed species to be dominant when they were present in at least two of the 3 replicates and with a mean score > 1 (Table A.1).

3.2.2 Climate data acquisition and processing

Climate data for the closest weather station for each site were provided by the Russian Research Institute of Hydrometeorological Information–World Data Centre (RIHMI-WDC) for BAR, CHE, KRA and TOM, or were collected and merged from National Oceanic and Atmospheric Administration (NOAA) and InfoSPACE for SAE and SAW. The weather stations were located 4–76 km from the study sites (Table 3.2). KRA is the farthest from its weather station but, since they are both located in a plain and in an homogeneous climatic unit, the data used are likely to be representative for the study site. SAE is located in the foothills of the Salair mountains range while the closest weather station is located in the adjacent plain. SAW is located in the Salair mountains range but the closest weather station is in the foothills. Thus, the

Table 3.3: Characteristics of the aspen (*Populus tremula* L.) forest study stands. Values displayed for pole and tree stages (i.e. diameter at 1.30 m > 7 cm and height > 1.3 m).

Site	Stand	Area	Trees	Aspen[a]	Density	Basal area	DBH (cm)		Height[b] (m)			Age[b] (years)			LAI[c]		
		(m^2)	(n)	(%)	(n ha^{-1})	(m^2 ha^{-1})	mean	se	n	mean	se	n	mean	se	n	mean	se
BAR	1	325	38	100	1169	18.6	13.4	0.8	24	11.0	0.5	5	26	3	5	4.94	0.57
	2	100	18	78	1800	47.8	17.0	1.7	13	11.8	1.1	5	32	5			
	3	130	27	100	2077	37.6	14.3	1.0	25	10.8	0.7	5	29	3			
	4	364	33	100	907	28.1	17.8	1.6	10	16.7	1.6	7	32	2			
CHE	1	1050	35	89	333	31.7	33.8	1.4	13	26.0	0.7	5	56	1	3	3.77	0.28
	2	800	33	91	413	38.7	33.6	1.4	11	26.6	0.9	5	60	1			
	3	899	41	100	456	42.7	34.3	0.6	10	31.4	0.8	5	70	2			
	4	183	30	100	1639	20.5	12.3	0.5	10	15.5	0.2	10	16	1			
KRA	1	463	29	100	626	41.1	28.5	0.9	12	21.6	1.6	5	53	2	5	3.84	0.33
	2	696	33	94	474	33.1	28.6	1.5	11	18.1	1.2	6	46	4			
	3	242	30	100	1237	55.7	21.8	1.9	8	16.5	1.8	5	44	6			
SAE	1	192	31	100	1615	32.6	15.4	0.8	10	15.9	1.1	5	37	7	4	5.07	0.59
	2	156	33	100	2115	28.8	12.8	0.5	12	15.5	0.6	7	32	8			
	3	192	37	100	1927	25.9	12.9	0.4	11	15.8	0.8	7	28	8			
	4	457	40	80	875	44.8	24.7	1.0	10	22.4	0.6	8	66	2			
SAW	1	240	33	100	1375	60.7	23.5	0.6	13	26.8	0.7	5	45	2	5	5.03	0.36
	2	350	37	86	1057	48.6	23.6	0.9	11	24.6	0.6	5	45	1			
	3	320	31	100	969	35.3	21.2	0.7	10	23.0	0.5	5	49	1			
	4	278	28	96	1007	36.7	21.2	0.7	5	22.4	0.7	5	48	1			
TOM	1	330	37	89	1121	59.6	25.1	1.1	19	21.5	1.6	5	74	3	5	2.94	0.46
	2	264	40	80	1515	37.0	16.5	1.0	16	14.3	1.2	5	30	2			
	3	420	36	89	857	37.4	22.6	1.1	15	18.8	1.7	5	73	4			

n: number of individuals; DBH: diameter at breast height (1.30 m); [a]Other tree species: mostly *Betula pendula* but also, very rarely, *Abies sibirica*, *Padus avium*, *Pinus sibirica* and *Pinus sylvestris*; [b]only aspen trees; [c]data averaged from the study stands 1–3

climate data used for these two sites might not exactly correspond to the actual conditions of the sites. Additionally, for SAE and SAW, climate data were collected from different sources and did not permit to construct continuous climatic series. To fill gaps in temperature, we used linear relations with the closest stations in the region. The relations obtained were of good quality (data not shown) and we used the reconstructed temperature series for the dendro-climatic analyses.

Soil moisture dynamics were simulated with the daily water budget model Biljou version 53 (Granier et al. 1999). Basically, Biljou is an iterative model where the variations in soil water content are calculated at a daily pace as:

$$\Delta W = P - In - T - E_{u+s} - D \tag{3.1}$$

where ΔW is the change in soil water content (W) between two successive days, P is the total precipitation, In is the rainfall interception by the tree vegetation cover, T is the tree transpiration estimated by the Peinman–Monteith equation (Monteith and Unsworth 2013), E_{u+s} is the sum of the transpiration from the understorey vegetation and the evaporation from the soil, and D is the drainage at the bottom of the soil profile explored by fine roots. The inputs of the model are daily climate data—minimum, maximum and mean temperature, total precipitation, wind speed, global radiation, and vapour pressure deficit—, vegetation related parameters—maximum leaf area index (LAI), budburst and leaf fall dates, vertical root distribution in the soil—as well as soil related parameters—water content at the field capacity (W_{fc}), water content at the wilting point (i.e. at pF 4.2; W_{wp}), apparent and real density, and macro- and micro-porosity. This model was calibrated at BAR and TOM where it reproduced accurately soil moisture dynamics (Chap. 4). We employed average values of the fitted input parameters of BAR and TOM (mostly soil porosity) for CHE and KRA. The values of the input parameters are shown in Table A.2.

Water stress is usually assumed to occur when the relative extractable soil water (REW), computed on the scale of the entire soil profile explored by fine roots, drops below 40 % of maximum extractable water (W_{fc}). Under this threshold, transpiration is gradually reduced due to stomatal closure (Granier et al. 1999; Sadras and Milroy 1996). The REW (dimensionless) was computed daily as:

$$REW_d = \frac{W_d - W_{wp}}{W_{fc}} \tag{3.2}$$

and the soil water deficit (SWD, in mm) as:

$$SWD_d = 0.4 \times W_{fc} - W_d \tag{3.3}$$

Finally, we computed a stress intensity index (I_s, dimensionless), cumulating the daily differences between REW and W_{fc} (Granier et al. 1999) from the beginning (i)

to the end (n) of the vegetation season:

$$I_s = \sum_{d=i}^{n} \frac{SWD_d}{W_{fc}} \tag{3.4}$$

3.2.3 Tree core sampling and preparation, and ring-width measurement

On at least five dominant or co-dominant trees per stand, i.e. at least 15 trees per site, we collected a tree core at 1.3 m with a 5 mm diameter Pressler corer (Suunto). The tree cores were stored in the fridge until processing. They were mounted, cut to get a planned sectional view of the rings and dried at 60 °C before measurement of ring-width. The annual ring-widths were measured (precision 0.01 mm) using a binocular microscope fitted to a digitizing tablet coupled with a computer.

For the cores that did not reach pith, we estimated the distance to the pith from the last measured ring with the help of a sight of concentric circles. The number of lacking rings was computed dividing the distance to the pith by the average ring-width of the last five rings measured.

3.2.4 Analysis of the relations between radial growth, age, site and their variation in the last decades

For each tree core, we computed a chronology of 9 year centred rolling-mean of ring-width. These chronologies were first averaged by site to detect potential local effects on the regional scale of SW Siberia. They were then averaged by starting periods (based on the cambial age of the trees) to detect potential temporal evolution of growth levels. Three starting periods were chosen (1934–1954, 1955–1974 and 1975–2001) to achieve an optimum balance between growth category (as expected after the examination of the site average chronologies) representation and number of tree cores per period. This is an exploratory approach which aims at detecting general broad patterns. A dedicated sampling design would be necessary to adequately address any questions related to detecting temporal changes in growth patterns across sites.

3.2.5 Analysis of the relations between radial growth and climate related parameters

The individual ring-width series were crossdated using a moving graphic program after progressive detecting of so-called “pointer years” (defined as those years when at least 70 % of the series in a site present an absolute relative radial growth variation

Table 3.4: Description of the different analyses ran to investigate the relations between aspen radial growth and climate, or climate-related, variables.

Run	Time step	Variable(s) tested
Run 1	1 month	Temperature, Precipitation
Run 2	1 month	Temperature, Precipitation adapted[a]
Run 3	15 days[b]	Temperature, Precipitation adapted[a]
Run 4	15 days[c]	Temperature, Precipitation adapted[a]
Run 5	1 month	Relative extractable water[d]
Run 6	1 month	Stress intensity[d]
Run 7	1 month	Snow height
Run 8	1 month	Soil temperature at −20 cm

[a] winter precipitations set to 0 mm and released at snow-melt
[b] first period starting at snow-melt
[c] first period starting in March
[d] computed with the water budget model BILJOU

higher than 10 % relatively to the previous year; Becker et al. 1994). Some trees were eliminated from the analysis of the relations between radial growth and climate because they could not be crossdated with the majority of the trees from the same study site or because they were suppressed in their respective study stand and were poorly crossdated (Fig. A.1).

Individual tree-ring width series were subjected to detrending in order to remove the low frequency variability (so-called growth trend) that is due to biological or stand effects. The growth trend was computed using cubic splines with 50 % frequency cutoff of $0.67 \times L$ years, where L is the length (in years) of the longest individual chronology available for the site (Cook and Kairiukstis 1990; Cook and Peters 1981). The standardization was done by dividing each actual growth series by the growth trend to produce the ring-width index (RWI, dimensionless). A standard chronology was then built for each study site, averaging the individual RWI series using Tukey's biweight robust mean which minimize the effects of outliers (Mosteller and Tukey 1977). These standard chronologies were eventually truncated at their extremities to remove years with less than five samples.

A similar detrending procedure was applied to climate variables (air temperature, precipitation, snow height and soil temperature) for each site. The potential climatic trend was removed by a cubic spline with the same parameter as for ring-width. Climate indexes were computed by difference, for temperature, and by division, for precipitation and snow height, between actual measurement and index.

We explored the relations between tree growth and several climate indexes (air temperature, precipitation, snow height), or climate related indexes/variables (soil

temperature, soil relative extractable water content, water stress indexes) through several bootstrapped static correlation and response function analyses on monthly and 15 days time steps (see the description of these runs in Table 3.4). Relations were searched with the climate of the year of growth (year n) and from the previous year (year $n-1$). Correlation functions consist of Pearson's linear correlation estimates (Blasing et al. 1984). Response functions consist in indirect regression techniques that aim at mitigating the effects of predictor multicollinearity (Cropper 1984) by regressing the proxy record against the principal components of the climate data (Cook and Kairiukstis 1990; Fritts 1976). Robust parameters estimates were obtained by a bootstrap resampling procedure (Guiot 1991). We performed a stationary bootstrap resampling procedure—which accounts for temporal autocorrelation, resampling within blocks with a length chosen from a geometric distribution (Politis and Romano 1994; Politis and White 2004)—with 10 000 iterations. The significance of the bootstrap coefficients was tested at $p < 0.05$ by the percentile range method (Dixon 2001).

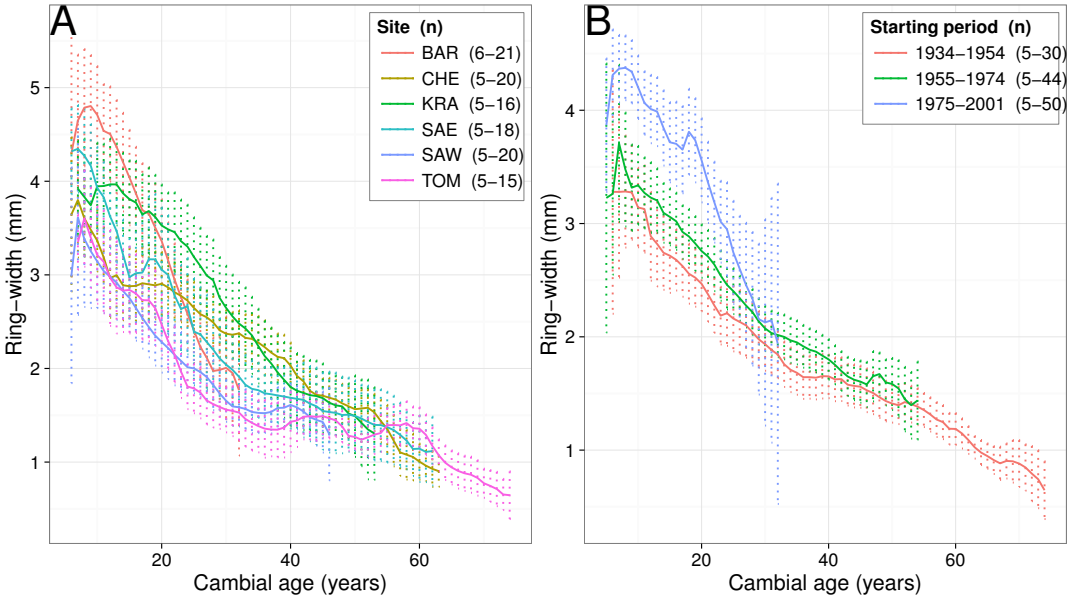
All data management and analyses were performed with R version 3.2.3 (R Core Team 2015). The detrending of the individual raw tree-ring width series and the construction of standard chronologies were performed with the R package *dplR* version 1.6.3 (Bunn 2008). The analyses of the relations between climate and tree growth were performed with the R package *treeclim* version 1.0.11 (Zang and Biondi 2015).

3.3 Results

3.3.1 Trends of aspen radial growth with ageing

All site chronologies (9 year rolling averages) presented a similar decreasing trend of radial growth with ageing (Fig. 3.1 A). BAR derived somehow from this trend since it presented a very high growth level in the first years but rapidly a strong decrease. The growth levels were different between sites, particularly in the first 30 years of growth: BAR, KRA and SAE exhibited the highest radial growth and SAW and TOM the lowest, CHE being in between (Fig. 3.1 A).

The three chronologies averaging tree radial growth per date of pith formation exhibited similar decreasing trends with ageing and different levels of growth between starting periods. The lower the cambial age was, the higher was the radial growth for a given age (Fig. 3.1 B). The most recent starting period (1975–2001) presented a sharper decrease in radial growth beyond 20 years, relatively to the other two periods.



Starting period	BAR	CHE	KRA	SAE	SAW	TOM	Sum
1934–1954	0	9	1	11	0	9	30
1955–1974	3	6	11	3	20	1	44
1975–2001	19	10	4	13	0	5	51
Sum	22	25	16	27	20	15	125

Figure 3.1: Aspen radial growth as a function of cambial age: site growth trends (A) and regional growth-trend variations over time (B). The values displayed are 9 years rolling-means of ring-width (lines) and 95 % confidence intervals (dotted ribbons) for at least $n = 5$ trees. The table below provides the number of trees (n) in each category (combination of site and starting period).

Table 3.5: Descriptive statistics of the ring-width and ring-width index chronologies.

	BAR	CHE	KRA	SAE	SAW	TOM
General						
First year	1979	1944	1956	1951	1964	1938
First year with > 5 trees	1984	1952	1965	1962	1967	1942
Last year with > 5 trees	2012	2011	2011	2012	2012	2011
Length of the standard chronology	29	60	47	51	46	70
Nb of trees	10	14	15	27	19	15
Average nb of trees per year	8.6	11.6	11.8	15.0	17.2	11.0
Nb of between-tree correlations	9	91	91	91	171	66
Ring-width length (RWL)						
Mean RWL (mm)	3.65	2.30	2.86	2.37	2.18	1.85
Median RWL (mm)	3.41	2.22	2.68	2.01	2.00	1.49
Standard deviation RWL (mm)	1.98	1.05	1.46	1.45	1.11	1.23
Mean interseries correlation	0.74	0.66	0.45	0.59	0.69	0.63
Expressed population signal	0.96	0.96	0.91	0.96	0.97	0.95
Signal to noise ratio	24.41	22.73	9.76	21.69	37.31	18.68
Mean sensitivity	0.31	0.27	0.30	0.27	0.29	0.44
Gini coefficient	0.28	0.24	0.24	0.24	0.24	0.31
First order auto-correlation	0.71	0.61	0.49	0.57	0.61	0.58
Ring-width index (RWI)						
Mean interseries correlation	0.41	0.44	0.35	0.45	0.56	0.49
Expressed population signal	0.86	0.90	0.86	0.93	0.96	0.91
Signal to noise ratio	5.93	9.21	6.36	12.43	21.45	10.68
Mean sensitivity	0.30	0.27	0.30	0.26	0.29	0.44
Gini coefficient	0.16	0.15	0.16	0.16	0.16	0.24
First order auto-correlation	0.09	0.20	0.18	0.31	0.21	0.31

3.3.2 Site growth chronologies

The age of the sampled trees in our study sites ranged from 13 to 79 years. The subsequent selection of trees, operated mainly at crossdating, allowed to construct standard chronologies of 29–70 years (Table 3.5 and Fig. 3.2). These chronologies may appear short with regard to most of dendrochronological studies, which present chronologies spanning over centuries, but they are the consequence of the life cycle of *P. tremula*. Our observations indicate that this species barely reaches the age of 100 years in SW Siberia, the trees of more than 80 years often being in a declining phase. Within each site, the sampled trees were correctly crossdated, as reflected by the mean inter-series correlations (0.45–0.74 for RWL and 0.35–0.56 for RWI; Table 3.5). Over the 1984–2012 common period, the sites presented no, or poor, cross-

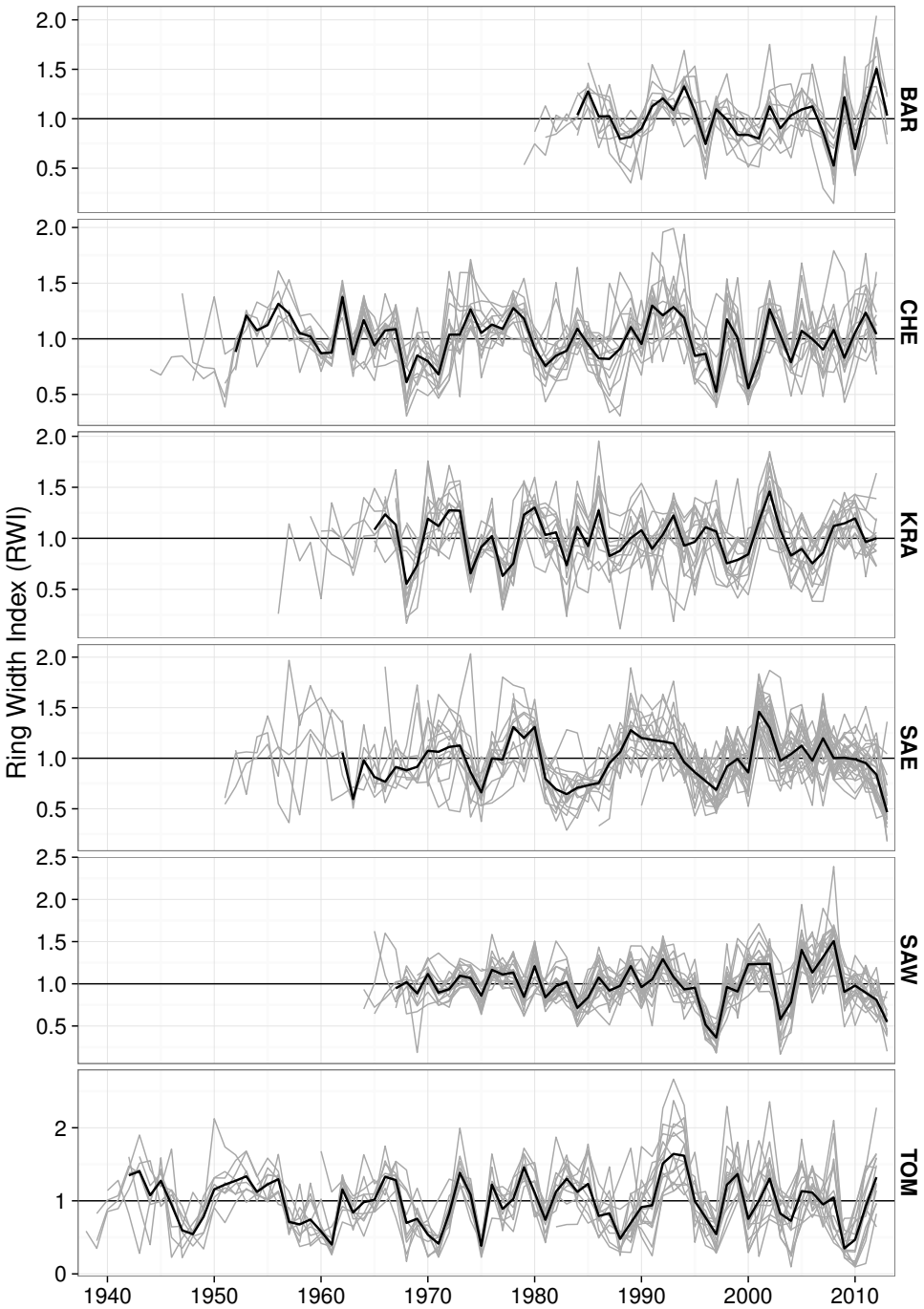


Figure 3.2: Ring-width index chronologies. Individual chronologies (tree by tree) are displayed in grey and standard chronologies (one per study site) are displayed in black. The standard chronologies are Tukey's biweight robust means over the longest periods containing at least 5 trees.

Table 3.6: Cross-correlation matrix of the aspen ring-width standard chronologies for the common period 1984–2012. Pearson's correlation coefficients. Values in boldface are statistically significant at the $p < 0.05$ level.

	CHE	KRA	SAE	SAW	TOM
BAR	0.21	−0.08	−0.26	−0.23	**0.42**
CHE		0.15	0.17	0.29	**0.59**
KRA			0.08	0.04	−0.03
SAE				**0.58**	0.08
SAW					0.25

correlations, except for TOM with BAR and CHE, and SAE with SAW (Table 3.6). This was also reflected by the relative asynchrony of the pointer years between sites (Fig. A.3). The important number of pointer years found for each site suggested they respond to climate variations. Mean sensitivities and Gini coefficients of all the sites were close (Table 3.5), indicating a similar tree-ring width (raw and detrended) diversity (Biondi and Qeadan 2008). The ring-width detrending greatly reduced the first-order auto-correlation for all sites, allowing the consideration of the potential climate effects in the year previous to tree-ring formation.

3.3.3 Relations between aspen radial growth and climate

Overall, the analysis following the correlation function procedure generally gave more significant climate regressors (Fig. 3.3) than following the response function procedure (Fig. A.2). Nevertheless, the results from these two procedures were rather concordant. Significant relations between radial growth and climate were found at KRA for almost all the variables tested while fewer relations were significant for the other sites, particularly for the year of the ring-formation (year n; Fig. 3.3).

At KRA, for the year n, aspen radial-growth responded positively to summer precipitations (run 1) and soil relative extractable water (REW) content (run 5) but negatively to summer water stress (run 6) and soil temperature (run 8; Fig. 3.3). Many significant relations were also found for the year previous to the ring formation (year $n-1$). In particular, a positive correlation was found when the winter ending in the year $n-1$ had a high snow cover (run 7), when the spring had high precipitations (run 1) and when the REW was high in spring and summer (run 5). On the contrary, high soil temperature (run 8) and stress intensity (run 6) in $n-1$ had a negative impact on radial-growth.

At BAR, aspen growth was only responsive to August precipitation in the year n (run 1; Fig. 3.3). Summer soil temperature tended to have a negative impact on growth but the results were not significant (run 8). In the response function analysis,

late summer stress had a significant negative impact on tree growth in the year n. Autumn soil temperature of $n-1$ (run 8) had negative impact while summer and October temperatures had a positive one. The snow negatively impacted growth in October from $n-1$ and in April from n (the latter only significant in the response function).

At CHE, tree growth was positively impacted by summer air temperature in n (run 1; Fig. 3.3). June and September precipitations in n tended to have a positive effect of growth but the relations were not significant (run 1). Winter precipitations (run 1) and snow height (run 7) in the previous year ($n-1$) had a positive effect on growth.

At TOM, air (run 1) and soil (run 8) temperatures in n had a positive effect on aspen radial-growth in summer but a negative effect in April (Fig. 3.3). Winter snow height of the previous year also had a positive impact on growth (run 7). From June $n-1$, high precipitations (run 1) and REW (run 5) had negative impacts on tree growth while temperature had positive ones.

At SAE and SAW, we were only able to test relations with air temperature (Fig. A.3). Temperature had positive effects at SAE at the beginning and the end of summer in n. It had a negative effect in autumn in n and positive effects in the winter preceding the growing season at SAW. High temperature in March $n-1$ also had a negative impact at SAW.

Finally, we note that the release of all winter precipitations at snow-melt (run 2), led to the same relations as those of run 1 (results not shown). Also, the analyses on shorter periods (15 days, runs 3 and 4) did not really improve our understanding of the relations between aspen radial-growth and climate in SW Siberia (Fig. A.4). But at CHE, they suggest that late June precipitations in the year n would have a positive effect on tree growth.

3.4 Discussion

3.4.1 Site growth-potential and evolution of growth in the recent decades

The chronologies of aspen ring-width suggest that our study sites have different growth potentials and that growth was enhanced over time (Fig. 3.1).

Difference in growth levels may reflect a variation in site fertility on the scale of SW Siberia. This variation would fit with the pedo-bio-climatic gradient found in this region; higher growth levels being observed in the south, or in the forest-steppe zone, and lower growth levels in the north, or in the sub-taiga zone. Only considering the climatic gradient, it could be inferred that such growth levels are related to the gradient of temperature since this factor is likely to play a major role in cold

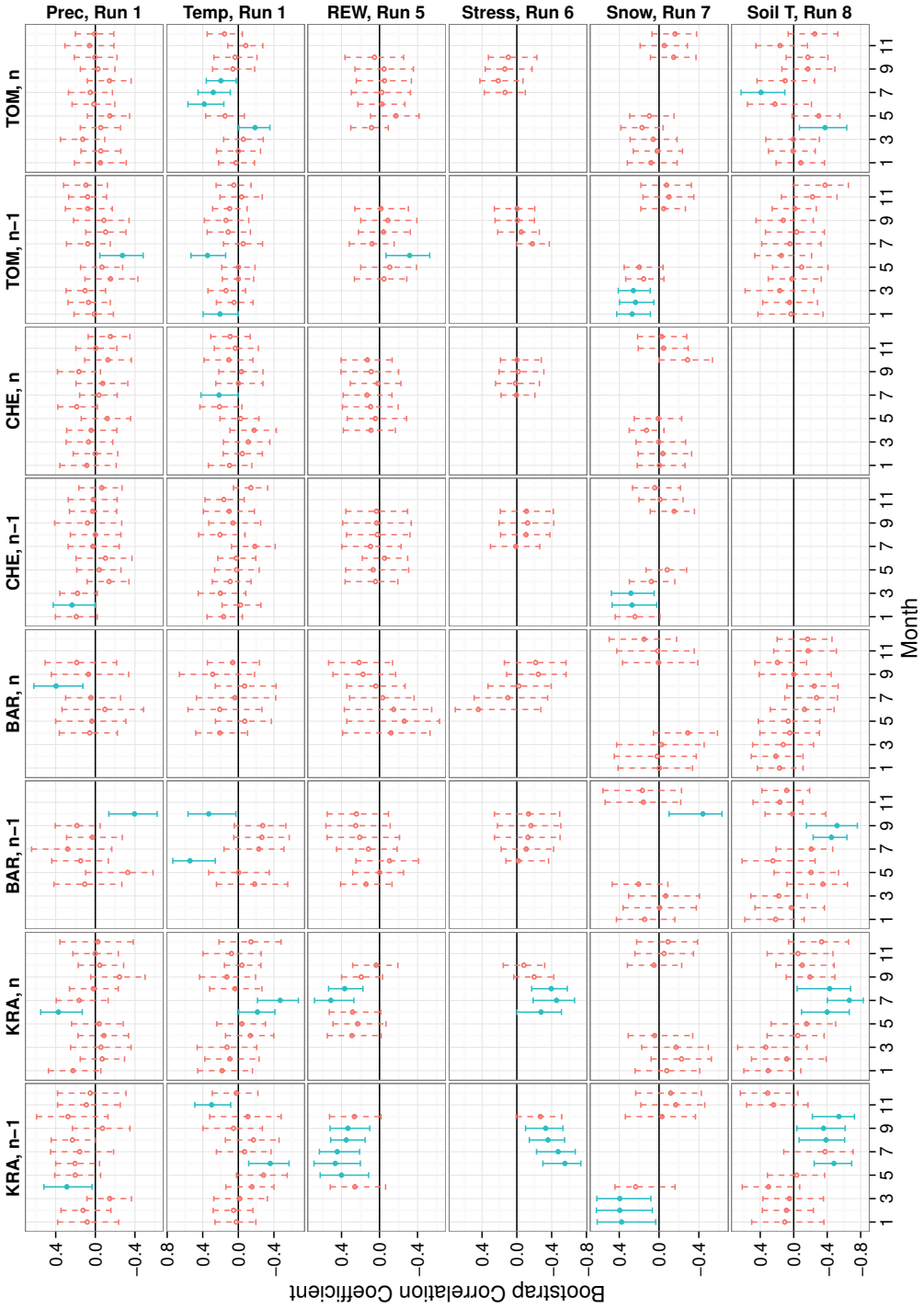


Figure 3.3: Plot of the bootstrapped correlation function analysis relating tree-ring growth to climate-related variables of the current (n) and the previous (n-1) year in four sites of SW Siberia. Significant coefficients, as judged by the bootstrapping procedure, are displayed in blue while non-significant coefficients are in red. The runs are described in Table 3.4.

or cold-temperate ecosystems. However, site fertility integrates the interactions between climate, soil, vegetation and other living organisms (e.g. micro-organisms).

The change of productivity during the 20th century is a widely observed phenomenon (Becker et al. 1995; Pretzsch et al. 2014). Several environmental factors can enhance tree growth, among which the rising of air temperatures (Briffa et al. 2008), increasing atmospheric CO_2 concentrations (Norby et al. 2005) and increasing atmospheric nitrogen (N) deposition (Fenn et al. 2003). These factors may interact (Baig et al. 2015; Feng et al. 2015) or be modulated by other environmental factors such as nutrient availability (Lukac et al. 2010; Norby et al. 2010; Reich et al. 2006; Wieder et al. 2015). The rising of temperatures and CO_2 levels are well documented for Northern Eurasia (IPCC 2013). If N deposition might occur at relatively low levels in SW Siberia (Dentener et al. 2006; Galloway et al. 2004), it is possible that its effects are not negligible since local ecosystem productivity is probably limited by N or by the timing of N availability (Chap. 7 and Brédoire et al. 2016a; Hedin 2004; Reich and Oleksyn 2004; Smurygin 1974). Finally, we were unaware of the evolution of the social status of the measured trees during their life, whereas it is the primary factor controlling growth level and responses to environmental conditions (Brienen et al. 2012). It is likely that a dominant tree at a given time has been less-dominant in earlier stages of its life (Becker et al. 1995). An exacerbation of this phenomenon can be expected in irregular forest stands (unmanaged forest with mixed species or mixed age classes) such as these aspen stands of SW Siberia mostly regenerating by suckering.

To prove and disentangle the effects of global change requires more thorough investigations. Our sampling design was not fully adapted to disentangle all the factors that may be implied in the control of these growth trends. First, some sites were over-represented in some birth categories and vice-versa (Fig. 3.1 table). For example, the rather diverging growth patterns with ageing of BAR, comparatively to the other sites, and of the most recent birth period, comparatively to the older periods, were probably related. In fact, BAR had a relatively high weight in the average chronology for the birth period 1975–2001 and almost all the trees from BAR belonged to the youngest birth period (Fig. 3.1 table). Ideally, the number of trees sampled should be much larger, the trees should be chosen in both dominant and co-dominant categories and the sample should be balanced, notably with regard to age classes, within and between sites (Becker et al. 1995).

3.4.2 Climate control of aspen stem radial growth

The information conveyed by the different runs we performed (Table 3.4) can be redundant (e.g. soil temperature is closely related to air temperature in the absence of a snow cover, REW and water stress are the result of precipitation and temperature). However, these runs were complementary, allowing the elaboration of finer

hypotheses on the control of climate on aspen radial growth in SW Siberia. As we expected, two groups of sites with different sensitivity to climate variables arose from our analyses. These two groups fit with the bioclimatic zones which were defined according to to climate and vegetation characteristics.

In steppe–forest-steppe, the driest areas of SW Siberia typically found in the south—here represented by KRA and BAR—, aspen stem radial growth was found to be sensitive to the climate variables controlling the soil moisture balance. Such responses were stronger in the driest site (KRA). Overall, tree growth benefits in such areas from summer precipitations and is impacted by the water budget of the preceding year. Drought, or water deficit, induces short-term physiological disorders—typically a decreased carbon and nutrient assimilation, and sometimes a deterioration of the photosynthetic machinery—that have to be repaired before the resume of normal processes (Bréda et al. 2006). The reduction of the carbohydrate reserves consecutive to a drought event impacts tree maintenance, growth—carbon allocation for growth is modified between leaf, root, branches and stem—and defence (e.g. against insect, frost and another drought damages) possibly over several years (Bréda et al. 2006). Also, nitrogen nutrition and cycling is likely to be modified by drought (Geißler et al. 2004). At KRA, tree growth benefits from high (relatively to the local averages) precipitations levels early in the season (June) which permit to maintain a high soil water content in summer, while high air and soil temperatures in summer, concomitant with intense and early water stress, are detrimental for tree growth (Fig. 3.3). Such inverse relations between summer temperature and tree growth were reported for *P. tremuloides* (Hanna and Kulakowski 2012; Leonelli et al. 2008) and other species with growth responsive to soil moisture (e.g. Abrams et al. 1998; Archambault and Bergeron 1992; Michelot et al. 2012). The soil moisture conditions in the preceding growing season also greatly impact stem radial growth, as reflected by the positive correlations with REW and the negative correlations with stress intensity. Such a response to soil moisture conditions of the preceding years has also been reported for *P. tremuloides* stands growing in Canada (Hogg et al. 2013; Huang et al. 2010). The positive impact of a high snow cover in the preceding season has probably to be related to the positive impact of high soil moisture content in the following growing season. In fact, the yearly soil moisture balance depends for a large part on the input of melt-water in the steppe and forest-steppe zones of SW Siberia (Chap. 4). By insulating soil, snow also protects fine roots from the damages of winter freezing and/or freeze–thaw cycles that occur in late winter–early spring (Cleavitt et al. 2008; Kreyling et al. 2012; Repo et al. 2014; Tierney et al. 2001). Such positive impacts of snow height have been reported for *P. tremuloides* (Hogg et al. 2002). However, we note that neither winter precipitations nor soil temperature from the previous year would confirm one of these mechanisms (no significant correlations were found). At BAR, late summer precipitations are beneficial to growth suggesting that trees are sensitive to water deficit but that this deficit usually occurs later and

is less intensive that at KRA. As for KRA, air and soil temperatures in summer tend to have negative impacts on aspen growth. Surprisingly, October precipitations from the previous year negatively impacted radial growth at BAR, in contradiction with the hypothesis developed regarding the water balance of the previous year. However, such a negative impact of October precipitations might not reflect the role of soil moisture content but a shortening of the vegetation season due to early winter arrival. In fact, there was no correlation with water stress in October $n-1$, temperature had a positive impact and snow a negative one. The same phenomenon, lengthening of the vegetation season permitted by higher temperatures, seems to occur at KRA but would not be coupled with snow height (no correlation) because snowfall never occurs in October in this area. Autumn months (end of September, beginning of October) are the time of leaf senescence in this area. Early freezing conditions and snowfall, occurring before the leaf senescence is complete, may alter the resorption of energy and nutrients that are essential for the subsequent leaf budding and could be detrimental to total growth during the next season, as suggested for quaking aspen (Landhäusser and Lieffers 2003). On the contrary, high October temperature in the previous year may avoid such phenomena and reduce number and intensity of the freeze–thaw cycle events, potentially inducing fine root damage and nutrient loss.

In the north of the forest-steppe (e.g. CHE) and in sub-taiga (e.g. TOM), typically in the north of SW Siberia or in the low mountain ranges like Salair (e.g. SAW), aspen radial growth is essentially controlled by summer air and soil temperatures (Fig. 3.3). This finding is coherent with many studies reporting that temperature is often one of the main climate factor limiting average tree growth in boreal ecosystems (Boisvenue and Running 2006; Seddon et al. 2016). The sub-taiga zone is positioned on the southern border of the Eurasian boreal forests. A possible explanation is that warmer temperatures enhance water absorption, and so nutrient absorption, due to increased hydraulic conductivity in the roots and decreased kinematic viscosity of water (Kramer and Kozlowski 1960). However, high April air and soil temperatures appeared to be detrimental for aspen growth at TOM and the same trend was found (but not significant) at CHE. A possible explanation would concern the loss of nutrients because snow-melt would occur too early with regard to vegetation growth initiation. Snow-melt is the main period of drainage in sub-taiga and can be important depending on the snow-mass accumulated in winter and on the soil water depletion in the previous year (Chap. 4). In the sites with relatively high snow-packs, such as TOM, the soil does not freeze (Chap. 4) and microbial activity is susceptible to continue over winter, accumulating nutrients in its biomass (Brooks and Williams 1999; Buckeridge and Grogan 2010). At melting, such microbial biomass could be lyzed, due to sudden change in temperature and moisture conditions, inducing a spring flush of nutrients in the soil solution (Buckeridge and Grogan 2008). In the case where vegetation is not active and the soil not able to adsorb the nutrients, the

nutrients might be lost from the system by drainage. Also, an early disappearance of the snow-pack induced by high late-winter temperature may expose the soil to several freeze–thaw cycles, also known to damage fine roots (Cleavitt et al. 2008; Kreyling et al. 2012; Repo et al. 2014; Tierney et al. 2001) and to enhance the release of nutrients (Brooks et al. 2010; Henry 2007) which, again, could be lost by high levels of drainage or high spring precipitations on a water-saturated soil. However, we note that the negative impacts of spring precipitations in the year n at TOM and CHE were not significant. Alternatively, an early rising of soil temperature may enhance microbial growth and thus immobilization of nutrients such as N which would not be readily available a few weeks later, when trees initiate seasonal activity. June precipitations from $n - 1$, together with REW, had negative impacts at TOM. Such relations may reflect nutrient losses because of drainage induced by an excess of precipitations, the negative impact of rainy (i.e. cloudy and rather cold) weather on plant phenology at the starting of the active vegetation season, or even detrimental impacts of excess water on fine roots experimenting anoxic conditions. For example, Imada et al. (2008) found that fine-root growth and the whole plant biomass production of *P. alba* were affected by the level of the water-table. At both CHE and TOM, aspen radial growth responded positively to high snow cover in the year prior to ring formation. This effect is rather difficult to explain. In fact, at least at TOM, no significant effect (or even a trend) of winter soil temperature was found, suggesting that the benefit would not come from a better soil thermal insulation. Additionally, an excess of June precipitation and soil water content, the latter being more probable after a high snow-pack, were detrimental for tree growth.

3.4.3 Potential impacts of global change

Altogether, we identified diverging responses of *P. tremula* stem radial growth to climate variables along our gradient of pedoclimatic conditions in SW Siberia. These findings have several implications for the prediction of Northern Eurasian forest productivity and community composition in the context of global change.

Our data suggest that aspen growth was enhanced over time during the 20th century. A possible explanation of such a phenomenon, if confirmed, concerns the rising of temperature which is likely to constitute one of the main controls on the average growth of aspen in SW Siberia. However, whether this increase of temperature will continue to enhance growth in the next decades is rather uncertain. In fact, tree growth is modulated by several other factors, such as site fertility which integrates the temporal dynamics of climate and nutrient availability.

Concerning our study area, we can infer that the rising of temperature might continue to enhance aspen stem radial growth in the northern areas, i.e. in the current sub-taiga bioclimatic zone, because of longer vegetation season, alleviation of temperature limitation during the vegetation season and since the soil water moisture

content would remain at a sufficient level. By contrast, in the southern areas, i.e. the current steppe and forest-steppe bioclimatic zones, it is likely that water-shortage, but also potentially temperature higher than the optimum for aspen physiological functioning, would become increasingly detrimental. In such places, extreme drought events might induce aspen forest stand declines and disappearance of the species. Interestingly, the water budget of SW Siberia is likely to be increasingly dependant on the amount of snowfall at wintertime. These amounts have been projected to increase with climate change (Bulygina et al. 2011, 2010, 2009) but high uncertainty remains on these projections (Groisman et al. 2014). In addition, some simulations we performed suggested that the frequency of incomplete recharge of the soil water capacity would increase even with increasing snow amounts, depending on the intensity of the discharge in the previous summer (Chap. 4). Altered soil temperature and moisture conditions, which are usually very contrasting between seasons in SW Siberia, may also modify biogeochemical cycles and so nutrient availability in directions and amplitudes difficult to predict. Altogether these changes will probably participate to modifications in the vegetation community composition and ecosystem primary productivity.

Further investigations with improved sampling designs (Nehrbass-Ahles et al. 2014) and additional variables measured (Foster et al. 2015) should allow building projections on growth and productivity of *P. tremula*. Finally, if changing climatic conditions may allow aspen to cover new and wide areas in the next decades (Shuman et al. 2015), a great uncertainty associated with the importance of soil characteristics remains since the soils of the current taiga zones are intrinsically different from the soils of SW Siberia (Jones et al. 2009).

Acknowledgements

F. Gérémia gave great support for tree core preparation, measurement of ring-width and crossdating. C. Zang provided a custom version of the R package *treeclim* version 1.0.11 with 10 000 bootstrap resampling iterations.

References

Abrams, M. C., Ruffner, C. M., and Morgan, T. A. (1998). Tree-ring responses to drought across species and contrasting sites in the ridge and valley of Central Pennsylvania. *Forest Science* 44.4, 550–558.

Alcamo, J., Dronin, N., Endejan, M., Golubev, G., and Kirilenko, A. (2007). A new assessment of climate change impacts on food production shortfalls and water availability in Russia. *Global Environmental Change* 17.3-4, 429–444. DOI: 10.1016/j.gloenvcha.2006.12.006.

Archambault, S. and Bergeron, Y. (1992). An 802-year tree-ring chronology from the Quebec boreal forest. *Canadian Journal of Forest Research* 22.5, 674–682. DOI: 10.1139/x92-090.

Baig, S., Medlyn, B. E., Mercado, L. M., and Zaehle, S. (2015). Does the growth response of woody plants to elevated CO_2 increase with temperature? A model-oriented meta-analysis. *Global Change Biology* 21.12, 4303–4319. DOI: 10.1111/gcb.12962.

Becker, M., Bert, G. D., Bouchon, J., Dupouey, J. L., Picard, J. F., and Ulrich, E. (1995). Forest decline and atmospheric deposition effects in the French mountains. In: chap. Long-term changes in forest productivity in northeastern France: the dendroecological approach, 143–156.

Becker, M., Nieminen, T., and Gérémia, F. (1994). Short-term variations and long-term changes in oak productivity in northeastern France. The role of climate and atmospheric CO_2. *Annals of Forest Science* 51.5, 477–492. DOI: 10.1051/forest:19940504.

Biondi, F. and Qeadan, F. (2008). Inequality in paleorecords. *Ecology* 89.4, 1056–1067. DOI: 10.1890/07-0783.1.

Blasing, T. J., Solomon, A. M., and Duvick, D. N. (1984). Response functions revisited. *Tree Ring Bulletin* 44, 1–15.

Boisvenue, C. and Running, S. W. (2006). Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. *Global Change Biology* 12.5, 862–882. DOI: 10.1111/j.1365-2486.2006.01134.x.

Brandt, J., Cerezke, H., Mallett, K., Volney, W., and Weber, J. (2003). Factors affecting trembling aspen (Populus tremuloides Michx.) health in the boreal forest of Alberta, Saskatchewan, and Manitoba, Canada. *Forest Ecology and Management* 178.3, 287–300. DOI: 10.1016/s0378-1127(02)00479-6.

Braun-Blanquet, J., Conard, H. S., and Fuller, G. D. (1932). *Plant sociology—the study of plant communities—authorized English translation of Pflanzensoziologie, by Dr. J. Braun-Blanquet. Translated, revised and edited by George D. Fuller and Henry S. Conard.* McGraw-Hill book company, inc. DOI: 10.5962/bhl.title.7161.

Bréda, N., Huc, R., Granier, A., and Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* 63.6, 625–644. DOI: 10.1051/forest:2006042.

Brienen, R. J. W., Gloor, E., and Zuidema, P. A. (2012). Detecting evidence for CO_2 fertilization from tree ring studies: The potential role of sampling biases. *Global Biogeochemical Cycles* 26.1. DOI: 10.1029/2011gb004143.

Briffa, K. R., Shishov, V. V., Melvin, T. M., Vaganov, E. A., Grudd, H., Hantemirov, R. M., Eronen, M., and Naurzbaev, M. M. (2008). Trends in recent temperature and radial tree growth spanning 2000 years across northwest Eurasia. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1501, 2269–2282. DOI: 10.1098/rstb.2007.2199.

Brooks, J. R., Barnard, H. R., Coulombe, R., and McDonnell, J. J. (2010). Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience* 3.2, 100–104. DOI: 10.1038/ngeo722.

Brooks, P. D., Grogan, P., Templer, P. H., Groffman, P., Öquist, M. G., and Schimel, J. (2011). Carbon and nitrogen cycling in snow-covered environments. *Geography Compass* 5.9, 682–699. DOI: 10.1111/j.1749-8198.2011.00420.x.

Brooks, P. D. and Williams, M. W. (1999). Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrological Processes* 13.14–15, 2177–2190. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2177::AID-HYP850>3.0.CO;2-V.

Buckeridge, K. M. and Grogan, P. (2008). Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. *Applied Soil Ecology* 39.2, 210–222. DOI: 10.1016/j.apsoil.2007.12.010.

Buckeridge, K. M. and Grogan, P. (2010). Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. *Biogeochemistry* 101.1-3, 105–121. DOI: 10.1007/s10533-010-9426-5.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Korshunova, N. N. (2011). Changes in snow cover characteristics over Northern Eurasia since 1966. *Environmental Research Letters* 6.4, 045204. DOI: 10.1088/1748-9326/6/4/045204.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Radionov, V. F. (2010). Snow cover basal ice layer changes over Northern Eurasia since 1966. *Environmental Research Letters* 5.1, 015004. DOI: 10.1088/1748-9326/5/1/015004.

Bulygina, O. N., Razuvaev, V. N., and Korshunova, N. N. (2009). Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters* 4.4, 045026. DOI: 10.1088/1748-9326/4/4/045026.

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia* 26.2, 115–124. DOI: 10.1016/j.dendro.2008.01.002.

Cervera, M. T., Storme, V., Soto, A., Ivens, B., Montagu, M. V., Rajora, O. P., and Boerjan, W. (2005). Intraspecific and interspecific genetic and phylogenetic relationships in the genus Populus based on AFLP markers. *Theoretical and Applied Genetics* 111.7, 1440–1456. DOI: 10.1007/s00122-005-0076-2.

Chen, H. Y., Klinka, K., and Kabzems, R. D. (1998). Site index, site quality, and foliar nutrients of trembling aspen: relationships and predictions. *Canadian Journal of Forest Research* 28.12, 1743–1755. DOI: 10.1139/x98-154.

Chen, H. Y., Krestov, P. V., and Klinka, K. (2002). Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. *Canadian Journal of Forest Research* 32.1, 112–119. DOI: 10.1139/x01-179.

Chimner, R. and Welker, J. (2005). Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixedgrass Prairie, WY, USA. *Biogeochemistry* 73.1, 257–270. DOI: 10.1007/s10533-004-1989-6.

Cleavitt, N. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Henry, K. S., and Driscoll, C. T. (2008). Effects of soil freezing on fine roots in a northern hardwood forest. *Canadian Journal of Forest Research* 38.1, 82–91. DOI: 10.1139/x07-133.

Cook, E. R. and Kairiukstis, L. A., eds. (1990). *Methods of Dendrochronology*. Springer Science + Business Media. DOI: 10.1007/978-94-015-7879-0.

Cook, E. R. and Peters, K. (1981). The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-ring Bulletin* 41, 45–53.

Cropper, J. P. (1984). Multicollinearity within selected western North American temperature and precipitation data sets. *Tree Ring Bulletin* 44, 29–37.

Dentener, F., Drevet, J., Lamarque, J. F., Bey, I., Eickhout, B., Fiore, A. M., Hauglustaine, D., Horowitz, L. W., Krol, M., Kulshrestha, U. C., Lawrence, M., Galy-Lacaux, C., Rast, S., Shindell, D., Stevenson, D., Noije, T. V., Atherton, C., Bell, N., Bergman, D., Butler, T., Cofala, J., Collins, B., Doherty, R., Ellingsen, K., Galloway, J., Gauss, M., Montanaro, V., Müller, J. F., Pitari, G., Rodriguez, J., Sanderson, M., Solmon, F., Strahan, S., Schultz, M., Sudo, K., Szopa, S., and Wild, O. (2006). Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation. *Global Biogeochemical Cycles* 20.4. DOI: 10.1029/2005gb002672.

Dickmann, D. I. and Kuzovkina, J. (2008). Poplars and willows of the world, with emphasis on silviculturally important species. In: *Poplars and willows: trees for society and the environment*, 8–91. DOI: 10.1079/9781780641089.0008.

Dixon, P. M. (2001). The encyclopedia of environmetrics. In: chap. Bootstrap resampling, 212–220.

Eckenwalder, J. E. (1996). Biology of Populus and its Implications for Management and Conservation. In: Part I. Chap. Systematics and evolution of Populus, 7–32.

Feng, Z., Rütting, T., Pleijel, H., Wallin, G., Reich, P. B., Kammann, C. I., Newton, P. C., Kobayashi, K., Luo, Y., and Uddling, J. (2015). Constraints to nitrogen acquisition of terrestrial plants under elevated CO_2. *Global Change Biology* 21.8, 3152–3168. DOI: 10.1111/gcb.12938.

Fenn, M. E., Baron, J. S., Allen, E. B., Rueth, H. M., Nydick, K. R., Geiser, L., Bowman, W. D., Sickman, J. O., Meixner, T., Johnson, D. W., and Neitlich, P. (2003). Ecological Effects of Nitrogen Deposition in the Western United States. *BioScience* 53.4, 404. DOI: 10.1641/0006-3568(2003)053[0404:eeondi]2.0.co;2.

Foster, J. R., Finley, A. O., D'amato, A. W., Bradford, J. B., and Banerjee, S. (2015). Predicting tree biomass growth in the temperate-boreal ecotone: is tree size, age, competition or climate response most important? *Global Change Biology*. DOI: 10.1111/gcb.13208.

Fritts, H. C. (1976). *Tree rings and climate*. Academic Press, p. 567.

Galloway, J., Dentener, F., Capone, D., Boyer, E., Howarth, R., Seitzinger, S., Asner, G., Cleveland, C., Green, P., Holland, E., Karl, D., Michaels, A., Porter, J., Townsend, A., and Vöosmarty, C. (2004). Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70 (2), 153–226. DOI: 10.1007/s10533-004-0370-0.

Geißler, A., Keitel, C., Nahm, M., and Rennenberg, H. (2004). Water Shortage Affects the Water and Nitrogen Balance in Central European Beech Forests. *Plant Biology* 6.3, 289–298. DOI: 10.1055/s-2004-820878.

Gordov, E. P. and Vaganov, E. A. (2010). Siberia integrated regional study: multidisciplinary investigations of the dynamic relationship between the Siberian environment and global climate change. *Environmental Research Letters* 5.1, 015007. DOI: 10.1088/1748-9326/5/1/015007.

Granier, A., Bréda, N., Biron, P., and Villette, S. (1999). A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* 116.2–3, 269–283. DOI: 10.1016/S0304-3800(98)00205-1.

Grippa, M., Kergoat, L., Toan, T. L., Mognard, N. M., Delbart, N., L'Hermitte, J., and Vicente-Serrano, S. M. (2005). The impact of snow depth and snowmelt on the vegetation variability over central Siberia. *Geophysical Research Letters* 32.21. DOI: 10.1029/2005gl024286.

Groisman, P. Y. and Gutman, G., eds. (2012). *Regional Environmental Changes in Siberia and Their Global Consequences*. Springer Science + Business Media. DOI: 10.1007/978-94-007-4569-8.

Groisman, P. Y., Bogdanova, E. G., Alexeev, V. A., Cherry, J. E., and Bulygina, O. N. (2014). Impact of snowfall measurement deficiencies on quantification of precipitation and its trends over Northern Eurasia. *Ice and Snow* 126.2, 29. DOI: 10.15356/2076-6734-2014-2-29-43.

Groisman, P. Y., Blyakharchuk, T. A., Chernokulsky, A. V., Arzhanov, M. M., Marchesini, L. B., Bogdanova, E. G., Borzenkova, I. I., Bulygina, O. N., Karpenko, A. A., Karpenko, L. V., Knight, R. W., Khon, V. C., Korovin, G. N., Meshcherskaya, A. V., Mokhov, I. I., Parfenova, E. I., Razuvaev, V. N., Speranskaya, N. A., Tchebakova, N. M., and Vygodskaya, N. N. (2012). Climate changes in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 3, 57–109. DOI: 10.1007/978-94-007-4569-8_3.

Groisman, P. Y., Knight, R. W., Razuvaev, V. N., Bulygina, O. N., and Karl, T. R. (2006). State of the ground: Climatology and changes during the past 69 Years over Northern Eurasia for a rarely used measure of snow cover and frozen land. *Journal of Climate* 19.19, 4933–4955. DOI: 10.1175/JCLI3925.1.

Groisman, P. and Soja, A. J. (2009). Ongoing climatic change in Northern Eurasia: justification for expedient research. *Environmental Research Letters* 4.4, 045002. DOI: 10.1088/1748-9326/4/4/045002.

Guiot, J. (1991). The bootstrapped response function. *Tree Ring Bulletin* 51, 39–41.

Hajek, P., Hertel, D., and Leuschner, C. (2013). Intraspecific variation in root and leaf traits and leaf-root trait linkages in eight aspen demes (Populus tremula and P. tremuloides). *Frontiers in Plant Science* 4. DOI: 10.3389/fpls.2013.00415.

Hamrick, J. (2004). Response of forest trees to global environmental changes. *Forest Ecology and Management* 197.1-3, 323–335. DOI: 10.1016/j.foreco.2004.05.023.

Hanna, P. and Kulakowski, D. (2012). The influences of climate on aspen dieback. *Forest Ecology and Management* 274, 91–98. DOI: 10.1016/j.foreco.2012.02.009.

Hardy, J. P., Groffman, P. M., Fitzhugh, R. D., Henry, K. S., Welman, A. T., Demers, J. D., Fahey, T. J., Driscoll, C. T., Tierney, G. L., and Nolan, S. (2001). Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56 (2), 151–174. DOI: 10.1023/A:1013036803050.

Hedin, L. O. (2004). Global organization of terrestrial plant-nutrient interactions. *Proceedings of the National Academy of Sciences* 101.30, 10849–10850. DOI: 10.1073/pnas.0404222101.

Hemming, J. D. C. and Lindroth, R. L. (1999). Effects of Light and Nutrient Availability on Aspen: Growth, Phytochemistry, and Insect Performance. *Journal of Chemical Ecology* 25.7, 1687–1714. DOI: 10.1023/a:1020805420160.

Henry, H. A. (2007). Soil freeze–thaw cycle experiments: Trends, methodological weaknesses and suggested improvements. *Soil Biology and Biochemistry* 39.5, 977–986. DOI: 10.1016/j.soilbio.2006.11.017.

Hogg, E. H., Brandt, J. P., and Kochtubajda, B. (2002). Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research* 32.5, 823–832. DOI: 10.1139/x01-152.

Hogg, E. (1999). Simulation of interannual responses of trembling aspen stands to climatic variation and insect defoliation in western Canada. *Ecological Modelling* 114.2-3, 175–193. DOI: 10.1016/s0304-3800(98)00150-1.

Hogg, E., Barr, A., and Black, T. (2013). A simple soil moisture index for representing multi-year drought impacts on aspen productivity in the western Canadian interior. *Agricultural and Forest Meteorology* 178-179, 173–182. DOI: 10.1016/j.agrformet.2013.04.025.

Huang, J., Tardif, J. C., Bergeron, Y., Denneler, B., Berninger, F., and Girardin, M. P. (2010). Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology* 16.2, 711–731. DOI: 10.1111/j.1365-2486.2009.01990.x.

Húlten, E. and Fries, M. (1986). *Atlas of North European Vascular Plants North of the Tropic of Cancer*. Vol. 1–3. Koeltz Scientific Books, p. 1172.

Imada, S., Yamanaka, N., and Tamai, S. (2008). Water table depth affects Populus alba fine root growth and whole plant biomass. *Functional Ecology* 22.6, 1018–1026. DOI: 10.1111/j.1365-2435.2008.01454.x.

Ingvarsson, P. K. (2005). Nucleotide Polymorphism and Linkage Disequilibrium Within and Among Natural Populations of European Aspen (Populus tremula L., Salicaceae). *Genetics* 169.2, 945–953. DOI: 10.1534/genetics.104.034959.

IPCC (2013). *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Ed. by T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. Midgley. Cambridge Books Online. Cambridge University Press. 1535 pp. DOI: 10.1017/CBO9781107415324.

IUSS Working Group WRB (2014). *World Reference Base for Soil Resources 2014 - International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106.* FAO.

Iwata, Y., Hayashi, M., Suzuki, S., Hirota, T., and Hasegawa, S. (2010). Effects of snow cover on soil freezing, water movement, and snowmelt infiltration: A paired plot experiment. *Water Resources Research* 46.9. DOI: 10.1029/2009wr008070.

Jansson, S. and Douglas, C. J. (2007). Populus: A Model System for Plant Biology. *Annual Review of Plant Biology* 58.1, 435–458. DOI: 10.1146/annurev.arplant.58.032806.103956.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J. (2012). Uncertainty analysis of vegetation distribution in the northern high latitudes during the

21st century with a dynamic vegetation model. *Ecology and Evolution* 2.3, 593–614. DOI: 10.1002/ece3.85.

Johansson, T. (1996). Site index curves for European aspen (Populus tremula L.) growing on forest land of different soils in Sweden. *Silva Fennica* 30.4, 437–458. DOI: 10.14214/sf.a8503.

Johansson, T. (2002). Increment and biomass in 26- to 91-year-old European aspen and some practical implications. *Biomass and Bioenergy* 23.4, 245–255. DOI: 10.1016/s0961-9534(02)00056-9.

Jones, A., Stolbovoy, V., Tarnocai, C., Broll, G., Spaargaren, O., and Montanarella, L., eds. (2009). *Soil Atlas of the Northern Circumpolar Region*. European Commission, Office for Official Publications of the European Communities, p. 142. DOI: 10.2788/95795.

Karacic, A. and Weih, M. (2006). Variation in growth and resource utilisation among eight poplar clones grown under different irrigation and fertilisation regimes in Sweden. *Biomass and Bioenergy* 30.2, 115–124. DOI: 10.1016/j.biombioe.2005.11.007.

Kemperman, J. A. and Barnes, B. V. (1976). Clone size in American aspens. *Canadian Journal of Botany* 54.22, 2603–2607. DOI: 10.1139/b76-280.

Kirdyanov, A., Hughes, M., Vaganov, E., Schweingruber, F., and Silkin, P. (2003). The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees* 17, 61–69. DOI: 10.1007/s00468-002-0209-z.

Kouki, J., Arnold, K., and Martikainen, P. (2004). Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. *Journal for Nature Conservation* 12.1, 41–52. DOI: 10.1016/j.jnc.2003.08.002.

Kramer, P. J. and Kozlowski, T. T. (1960). *Physiology of trees*. McGraw-Hill Book Co., Inc.

Kreyling, J., Peršoh, D., Werner, S., Benzenberg, M., and Wöllecke, J. (2012). Short-term impacts of soil freeze-thaw cycles on roots and root-associated fungi of Holcus lanatus and Calluna vulgaris. *Plant and Soil* 353 (1-2), 19–31. DOI: 10.1007/s11104-011-0970-0.

Landhäusser, S. M. and Lieffers, V. J. (2003). Seasonal changes in carbohydrate reserves in mature northern Populus tremuloides clones. *Trees - Structure and Function* 17.6, 471–476. DOI: 10.1007/s00468-003-0263-1.

Laureysens, I., Temmerman, L. D., Hastir, T., Gysel, M. V., and Ceulemans, R. (2005). Clonal variation in heavy metal accumulation and biomass production in a poplar coppice culture. II. Vertical distribution and phytoextraction potential. *Environmental Pollution* 133.3, 541–551. DOI: 10.1016/j.envpol.2004.06.013.

Leonelli, G., Denneler, B., and Bergeron, Y. (2008). Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Canadian Journal of Forest Research* 38.5, 1211–1222. DOI: 10.1139/x07-227.

Lukac, M., Calfapietra, C., Lagomarsino, A., and Loreto, F. (2010). Global climate change and tree nutrition: effects of elevated CO_2 and temperature. *Tree Physiology* 30.9, 1209–1220. DOI: 10.1093/treephys/tpq040.

Messaoud, Y. and Chen, H. Y. H. (2011). The Influence of Recent Climate Change on Tree Height Growth Differs with Species and Spatial Environment. *PLoS ONE* 6.2, e14691. DOI: 10.1371/journal.pone.0014691.

Michaelian, M., Hogg, E. H., Hall, R. J., and Arsenault, E. (2011). Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology* 17.6, 2084–2094. DOI: 10.1111/j.1365-2486.2010.02357.x.

Michelot, A., Bréda, N., Damesin, C., and Dufrêne, E. (2012). Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *Forest Ecology and Management* 265, 161–171. DOI: 10.1016/j.foreco.2011.10.024.

Monteith, J. L. and Unsworth, M. H. (2013). Steady-state heat balance. In: *Principles of Environmental Physics*, 217–247. DOI: 10.1016/b978-0-12-386910-4.00013-5.

Mooney, H. A., Drake, B. G., Luxmoore, R. J., Oechel, W. C., and Pitelka, L. F. (1991). Predicting ecosystem responses to elevated CO_2 concentrations. *BioScience* 41.2, 96–104. DOI: 10.2307/1311562.

Morgan, J. A., Pataki, D. E., Körner, C., Clark, H., Grosso, S. J. D., Grünzweig, J. M., Knapp, A. K., Mosier, A. R., Newton, P. C. D., Niklaus, P. A., Nippert, J. B., Nowak, R. S., Parton, W. J., Polley, H. W., and Shaw, M. R. (2004). Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia* 140.1, 11–25. DOI: 10.1007/s00442-004-1550-2.

Mosteller, F. and Tukey, J. (1977). *Data Analysis and Regression: A Second Course in Statistics*. Addison-Wesley Publishing Company.

Müller, A., Leuschner, C., Horna, V., and Zhang, C. (2012). Photosynthetic characteristics and growth performance of closely related aspen taxa: On the systematic relatedness of the Eurasian Populus tremula and the North American P. tremuloides. *Flora* 207.2, 87–95. DOI: 10.1016/j.flora.2011.11.001.

Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin, M., and Frank, D. (2014). The influence of sampling design on tree-ring-based quantification of forest growth. *Global Change Biology* 20.9, 2867–2885. DOI: 10.1111/gcb.12599.

Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E. (2010). CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences* 107.45, 19368–19373. DOI: 10.1073/pnas.1006463107.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R. (2005). Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* 102.50, 18052–18056. DOI: 10.1073/pnas.0509478102.

Pakull, B., Groppe, K., Meyer, M., Markussen, T., and Fladung, M. (2009). Genetic linkage mapping in aspen (Populus tremula L. and Populus tremuloides Michx.) *Tree Genetics and Genomes* 5.3, 505–515. DOI: 10.1007/s11295-009-0204-2.

Peng, Y. Y. and Dang, Q.-L. (2003). Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. *Forest Ecology and Management* 180.1-3, 1–9. DOI: 10.1016/s0378-1127(02)00486-3.

Politis, D. N. and Romano, J. P. (1994). The stationary bootstrap. *Journal of the American Statistical Association* 89, 1303–1313.

Politis, D. N. and White, H. (2004). Automatic Block-Length Selection for the Dependent Bootstrap. *Econometric Reviews* 23.1, 53–70. DOI: 10.1081/etc-120028836.

Pretzsch, H., Biber, P., Schütze, G., Uhl, E., and Rötzer, T. (2014). Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications* 5, 4967. DOI: 10.1038/ncomms5967.

R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Reich, P. B. and Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences* 101.30, 11001–11006. DOI: 10.1073/pnas.0403588101.

Reich, P. B., Hobbie, S. E., Lee, T., Ellsworth, D. S., West, J. B., Tilman, D., Knops, J. M. H., Naeem, S., and Trost, J. (2006). Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature* 440.7086, 922–925. DOI: 10.1038/nature04486.

Repo, T., Sirkiä, S., Heinonen, J., Lavigné, A., Roitto, M., Koljonen, E., Sutinen, S., and Finér, L. (2014). Effects of frozen soil on growth and longevity of fine roots of Norway spruce. *Forest Ecology and Management* 313, 112–122. DOI: 10.1016/j.foreco.2013.11.002.

Sadras, V. and Milroy, S. (1996). Soil-water thresholds for the responses of leaf expansion and gas exchange: A review. *Field Crops Research* 47.2-3, 253–266. DOI: 10.1016/0378-4290(96)00014-7.

Schepaschenko, D., McCallum, I., Shvidenko, A., Fritz, S., Kraxner, F., and Obersteiner, M. (2011). A new hybrid land cover dataset for Russia: a methodology for integrating statistics, remote sensing and in situ information. *Journal of Land Use Science* 6.4, 245–259. DOI: 10.1080/1747423x.2010.511681.

Schimel, D. S. (1995). Terrestrial ecosystems and the carbon cycle. *Global Change Biology* 1.1, 77–91. DOI: 10.1111/j.1365-2486.1995.tb00008.x.

Schimel, J. P., Bilbrough, C., and Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry* 36.2, 217–227. DOI: 10.1016/j.soilbio.2003.09.008.

Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., and Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*. DOI: 10.1038/nature16986.

Shepashenko, D., Shvidenko, A., and Nilsson, S. (1998). Phytomass (live biomass) and carbon of Siberian forests. *Biomass and Bioenergy* 14.1, 21–31. DOI: 10.1016/s0961-9534(97)10006-x.

Shiklomanov, A. I. and Lammers, R. B. (2009). Record Russian river discharge in 2007 and the limits of analysis. *Environmental Research Letters* 4.4, 045015. DOI: 10.1088/1748-9326/4/4/045015.

Shkolnik, I. M., Nadyozhina, E. D., Pavlova, T. V., Molkentin, E. K., and Semioshina, A. A. (2010). Snow cover and permafrost evolution in Siberia as simulated by the MGO regional climate model in the 20th and 21st centuries. *Environmental Research Letters* 5.1, 015005. DOI: 10.1088/1748-9326/5/1/01500510.1088/1748-9326/5/1/015005.

Shuman, J. K., Tchebakova, N. M., Parfenova, E. I., Soja, A. J., Shugart, H. H., Ershov, D., and Holcomb, K. (2015). Forest forecasting with vegetation models across Russia. *Canadian Journal of Forest Research* 45.2, 175–184. DOI: 10.1139/cjfr-2014-0138.

Smurygin, M. (1974). Basic trends of grassland research in the USSR. In: *Proceedings of the 12th International Grassland Congress. Moscow, Russia, 11–24 June 1974*, 76–88.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S., and Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56.3–4, 274–296. DOI: 10.1016/j.gloplacha.2006.07.028.

Soolanayakanahally, R. Y., Guy, R. D., Street, N. R., Robinson, K. M., Silim, S. N., Albrectsen, B. R., and Jansson, S. (2015). Comparative physiology of allopatric Populus species: geographic clines in photosynthesis, height growth, and carbon isotope discrimination in common gardens. *Frontiers in Plant Science* 6. DOI: 10.3389/fpls.2015.00528.

Suominen, O., Edenius, L., Ericsson, G., and Dios, V. R. de (2003). Gastropod diversity in aspen stands in coastal northern Sweden. *Forest Ecology and Management* 175.1-3, 403–412. DOI: 10.1016/s0378-1127(02)00142-1.

Tchebakova, N. M., Parfenova, E. I., Lysanova, G. I., and Soja, A. J. (2011a). Agroclimatic potential across central Siberia in an altered twenty-first century. *Environmental Research Letters* 6.4, 045207. DOI: 10.1088/1748-9326/6/4/045207.

Tchebakova, N. M., Parfenova, E. I., and Soja, A. J. (2011b). Climate change and climate-induced hot spots in forest shifts in central Siberia from observed data. *Regional Environmental Change* 11 (4), 817–827. DOI: 10.1007/s10113-011-0210-4.

Tchebakova, N. M., Parfenova, E., and Soja, A. J. (2009). The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4.4, 045013. DOI: 10.1088/1748-9326/4/4/045013.

Tchebakova, N. M., Rehfeldt, G. E., and Parfenova, E. I. (2010). From vegetation zones to climatypes: Effects of climate warming on Siberian ecosystems. In: *Permafrost Ecosystems. Siberian Larch Forests*. Chap. 22, 427–447.

Tierney, G., Fahey, T., Groffman, P., Hardy, J., Fitzhugh, R., and Driscoll, C. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56.2, 175–190. DOI: 10.1023/A:1013072519889.

Vaganov, E. A., Hughes, M. K., Kirdyanov, A. V., Schweingruber, F. H., and Silkin, P. P. (1999). Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature* 400.6740, 149–151.

van der Heijden, M. G. A., Bardgett, R. D., and van Straalen, N. M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* 11.3, 296–310. DOI: 10.1111/j.1461-0248.2007.01139.x.

Walker, M. D., Walker, D. A., Welker, J. M., Arft, A. M., Bardsley, T., Brooks, P. D., Fahnestock, J. T., Jones, M. H., Losleben, M., Parsons, A. N., Seastedt, T. R., and Turner, P. L. (1999). Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes* 13.14–15, 2315–2330. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2315::AID-HYP888>3.0.CO;2-A.

Wieder, W. R., Cleveland, C. C., Smith, W. K., and Todd-Brown, K. (2015). Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geoscience* 8.6, 441–444. DOI: 10.1038/ngeo2413.

Wipf, S. and Rixen, C. (2010). A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research* 29.1, 95–109. DOI: 10.1111/j.1751-8369.2010.00153.x.

Worrall, J. J., Marchetti, S. B., Egeland, L., Mask, R. A., Eager, T., and Howell, B. (2010). Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecology and Management* 260.5, 638–648. DOI: 10.1016/j.foreco.2010.05.020.

Yin, T., DiFazio, S. P., Gunter, L. E., Zhang, X., Sewell, M. M., Woolbright, S. A., Allan, G. J., Kelleher, C. T., Douglas, C. J., Wang, M., and Tuskan, G. A. (2008). Genome structure and emerging evidence of an incipient sex chromosome in Populus. *Genome Research* 18.3, 422–430. DOI: 10.1101/gr.7076308.

Zang, C. and Biondi, F. (2015). treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography* 38.4, 431–436. DOI: 10.1111/ecog.01335.

Zhang, T. (2005). Influence of the seasonal snow cover on the ground thermal regime: An overview. *Reviews of Geophysics* 43.4. DOI: 10.1029/2004rg000157.

Chapter 4

Is snow a hot variable? The control of soil temperature and moisture dynamics in south-western Siberia – Snow manipulation experiment and simulations of soil water budget

In collaboration with: A. Legout, M. R. Bakker, P. A. Barsukov, D. Derrien, Z. E. Kayler, P. Nikitich, O. Rusalimova, and B. Zeller.

4.1 Introduction

Siberia experiences a particularly strong climate change intensity on the global scale, but also on the scale of Northern Eurasia (Groisman et al. 2012; IPCC 2013). In the last century, annual mean surface air temperature raised by about 1.4 °C in Siberia. The warming trend was particularly strong in the cold season (November to March) (IPCC 2013). Mean annual precipitation was higher by about 10 % in the second than in the first half of the twentieth century, while precipitation amounts and the number of days with precipitation did not change in the following decades (end of 20th–beginning of 21st century). A significant redistribution by intensity among the days with precipitation occurred in the warm season (Groisman et al. 2012). Prolonged no-rain episodes (> 30 days) in summer were detected in the south of Siberia. Also, an increase in the cold season precipitation occurred over most of Siberia (IPCC 2013; Rawlins et al. 2010). Maximum snow depth, the number of days with more than 20 cm snow as well as the snow water equivalent have increased in the last decades over most of Siberia (Bulygina et al. 2010, 2009, 2007). Snow cover extent over Siberia did not appreciably change during winter (December–March) but it significantly retreated in spring–early summer, from April to June (Arndt et al. 2010; Bulygina et al. 2009; Groisman et al. 1994, 2006; Robinson et al. 1993; Takala et al. 2009). Climate projections indicate a further rise of temperatures and the trends observed for precipitations should be maintained with intensification of

phenomenons.

As a consequence of global change (climate change, rising atmospheric CO_2 concentration, etc.), substantial reshaping of Siberian ecosystems are expected (Groisman and Gutman 2012; Schaphoff et al. 2016). Bioclimatic zones have already been reported to move in space (Soja et al. 2007) and are projected to migrate northwards (Jiang et al. 2012; Kicklighter et al. 2014; Lucht et al. 2006; Shuman et al. 2015; Tchebakova et al. 2009, 2010). Changes in vegetation productivity are likely to occur but the direction of the change will be regional- and species-dependant (Schaphoff et al. 2016).

Site fertility is an important driver of vegetation productivity. It integrates the dynamics of climatic conditions and resources availability (water and nutrients) required for plant growth (Schoenholtz et al. 2000). In many ecosystems, nutrient limitation is a matter of availability for plants rather than total stock (Giehl and Wiren 2014). As the main repository of nutrients and water for plant uptake, soil is an important ecosystem compartment for the control of fertility. Water storage and availability are mainly dependent on soil physical properties (e.g. texture, structure) while nutrient availability is more dependent on soil chemical and biological properties. The size of the available pool of nutrients (soil solution and exchangeable/available pools) at a given time is of importance, but the processes that may replenish or flush this pool over time must also be considered (e.g. weathering, atmospheric deposition, nutrient leaching, biological cycling) (Legout et al. 2014; Ranger and Turpault 1999).

Soil temperature and moisture regimes control biological activity, that is responsible for the decomposition of organic matter, weathering of minerals, and thus for the release of nutrients for plant nutrition. Altered temperature and water availability, either in deficit or in excess, impair the mineral nutrition of plants by influencing nutrient availability and the physiology of uptake systems (Bassirirad 2000; Kreuzwieser and Gessler 2010; Rennenberg et al. 2009). Soil temperature and moisture regimes are the result of climatic conditions but are greatly modulated by soil properties as well as by soil cover properties (e.g. vegetation type and density, presence of snow). The latter control the fluxes of energy (e.g. albedo) and matter (e.g. water interception, evapo-transpiration) to and from the soil.

South-western (SW) Siberia is positioned on a gradient of climate, vegetation and soil conditions. It is the transition from the steppe (in the south) to the southern-taiga bioclimatic zones, through forest-steppe and sub-taiga. Typically, the south experiences warmer and drier conditions than the north (mean annual precipitation is about 300 mm in steppe against 600 mm in southern-taiga). In winter, the snowpack is higher, it sets up earlier and stands longer in the north. SW Siberia has historically been the most populated region of Siberia because of longer and warmer vegetation seasons and because of the presence of rich soils (e.g. Chernozems). In the context of global change, the fate of the agro-potential of such a region will be of

crucial interest. In spite of growing interest in Siberian ecosystems (e.g. Kicklighter et al. 2014; Tchebakova et al. 2011), a few functional ecological data are available in the international literature to assess soil processes. Especially, soil thermal and hydrological regimes are not well known.

With the global purpose to better assess nutrient availability in SW Siberia, this study aims: (1) to characterize the soil thermal and hydrological regimes in contrasting locations of south-western Siberia, (2) to assess which parameters are involved in regulating these regimes, (3) to elaborate realistic hypotheses on their evolution with global change, and (4) to discuss their potential impact on nutrient biogeochemistry and plant growth.

To achieve our goals, we selected two sites with contrasting pedoclimatic conditions. We monitored soil temperature and moisture under both aspen forest and grassland vegetation cover at both sites over more than two years. In order to study the impacts of the snow cover on these parameters, we artificially increased the height of the snow-pack on experimental plots. A water budget model (Biljou; Granier et al. 1999) was calibrated and employed to reconstruct the soil moisture content on the period 1966–2012 and to test climate change scenarii. In particular, we focussed on the possible changes in winter precipitation. Finally, on the basis of our results and making simple hypotheses, we initiated a discussion on the potential impacts of the soil thermal and hydrological regimes on nutrients biogeochemistry and plant growth and their potential evolution.

4.2 Materials and methods

4.2.1 Site description

Two sites were selected on the basis of their climatic and soil characteristics. We looked for places with contrasting climatic conditions, particularly in winter (different snow height). However, since soil and vegetation development also depend on climate, we opted for sites where the soil developed from a similar loess deposit and selected study plots with a similar vegetation cover in the two sites. We set up measurements and experiments under two types of vegetation: aspen forest (*Populus tremula* L.) and grassland.

The study sites were close to a weather station providing continuous, complete and qualitative climate archives. We had the possibility to set up a minimal installation of soil temperature and moisture monitoring. Also, these sites were rather accessible, notably during winter.

The site "BAR" is located in the vicinity of the city of Barnaul, in the forest-steppe zone, in the south of SW Siberia. Mean annual temperature is 2.7 °C (−14.1 °C in winter and 18.3 °C in summer), mean annual precipitation is 432 mm, the snow

height reaches in average 49 cm at the climax period and the snow season (> 1 cm) lasts in average 157 days (see Table 2.2 for more details). At BAR, the main soil forming processes are the formation and accumulation of organic matter, leaching of carbonates in the topsoil and formation of secondary carbonates in deep soil layers. Soil is classified as Haplic Phaeozem in forest and as Calcic Chernozem in grassland.

The site "TOM" is located in the vicinity of the city of Tomsk, in the sub-taiga zone, in the north of SW Siberia. Mean annual temperature is 0.9 °C (−15.6 °C in winter and 16.7 °C in summer), mean annual precipitation is 567 mm, the snow height reaches in average 71 cm at the climax period and the snow season (> 1 cm) lasts in average 178 days (see Table 2.2 for more details). At TOM, soil experiences water-table movements, with periodical saturation. Consequently, clays are washed from the topsoil and accumulate in the deeper layers, and carbonates have disappeared from the first metre of the soil profile. In addition, the litter decomposes faster than in forest-steppe and the accumulation of organic matter is lower at the soil surface. At this site, soil is classified as Albic Luvisol in forest and in grassland.

4.2.2 Monitoring of the soil physical status

Soil temperature

From autumn 2012, both forest and grassland of BAR and TOM were equipped with temperature data loggers (DS1921G Thermochron iButton, Maxim Integrated, USA). The temperature data loggers were set up at three soil depths, −5, −15, and −60 cm in holes or tranches made with the help of a soil corer or a spade. Two to four replicates were set up per site and vegetation cover. One to two temperature data loggers were also set up at 2 m above the soil surface on each site and for each vegetation cover. The temperature data loggers were changed regularly (usually every 6 months).

Soil volumetric water content

At spring 2013, both forest and grassland of BAR and TOM were equipped with soil volumetric water content (VWC) sensors (EC-5 Soil Moisture Sensor, Decagon, USA). Two depths, −15 and −60 cm, with ten replicates distributed between four soil pits, were set up. The soil pits were spaced by 5–20 m. Within a soil pit, the sensors were spaced by 0.5–1 m. Soil VWC was recorded every two hours. To improve the accuracy of field VWC measurements, we calibrated the EC-5 sensor with our study soils (details in Appendix B.1).

4.2.3 Snow manipulation on the field

In the winters 2013–2014 and 2014–2015, two snow applications were conducted in both vegetation covers at BAR (18/01/2014 and 22/02/2014, and 12/12/2014 and 23/01/2015) and TOM (22/12/2013 and 25/02/2014, and 04/12/2014 and 18/01/2015). The snow was moved from the surrounding area with the help of a snow blower (ST 656, Champion) and shovels.

The snow height on the experimental plots was recorded over the snow season with the help of temperature data loggers (DS1921G Thermochron iButton, Maxim Integrated, USA) set up on vertical sticks at 15, 30, 50, 75 and 100 cm.

4.2.4 Soil water budget modelling

On the two sites equipped with soil VWC sensors, BAR and TOM, we calibrated the water balance model Biljou version 53 (Granier et al. 1999). We performed water budget simulations only in our forest study plots for two reasons. Firstly, we were interested in the effects of climate and soil properties, which vary between our study sites but are rather similar between the two vegetation covers for a given site. Secondly, the model was developed for forest ecosystems.

Description of the model

Basically, Biljou is an iterative model where the variations in soil water content are calculated at a daily pace as:

$$\Delta W = P - In - T - E_{u+s} - D \tag{4.1}$$

where ΔW is the change in soil water content (W) between two successive days, P is the total precipitation, In is the rainfall interception by the tree vegetation cover, T is the tree transpiration estimated by the Peinman–Monteith equation (Monteith and Unsworth 2013), E_{u+s} is the sum of the transpiration from the understorey vegetation and the evaporation from the soil, and D is the drainage at the bottom of the soil profile explored by fine roots. Details on the computation of each of these parameters are given in Granier et al. (1999).

The inputs of the model are daily climate data—minimum, maximum and mean temperature, total precipitation, wind speed, global radiation, and vapour pressure deficit—, vegetation related parameters—maximum leaf area index (LAI), budburst and leaf fall dates, vertical root distribution in the soil—as well as soil related parameters—water content at the field capacity (W_{FC}), water content at the wilting point (i.e. at pF 4.2; W_{WP}), apparent and real density, and macro- and micro-porosity. Several soil layers can be implemented, for a given profile, in the model.

The model Biljou permits to assess conditions of soil drought, which induces water stress for plant functioning. A water stress is assumed to occur when the relative extractable soil water (REW), computed on the scale of the entire soil profile explored by fine roots, drops below 40 % of W_{FC}. Under this threshold, transpiration is gradually reduced due to stomatal closure (Granier et al. 1999; Sadras and Milroy 1996). The REW (dimensionless) is computed daily (d) as:

$$REW_d = \frac{W_d - W_{WP}}{W_{FC}} \tag{4.2}$$

and the soil water deficit (SWD, in mm) as:

$$SWD_d = 0.4 \times W_{FC} - W_d \tag{4.3}$$

When $REW < W_{FC}$, two stress indexes are computed, which can be cumulated over different periods: (i) the number of days of water stress, and (ii) the stress intensity (I_s, dimensionless), which cumulates the difference between REW and W_{FC} between the days i and n (e.g. defining a month, a season, a year, etc.):

$$I_s = \sum_{d=i}^{n} \frac{SWD_d}{W_{FC}} \tag{4.4}$$

Climate data acquisition and preparation

Most of the climate data were obtained from the Russian Research Institute of Hydrometeorological Information–World Data Centre (RIHMI-WDC) for the closest weather station (4 and 38 km away from the study sites BAR and TOM, respectively). The wind speed at 2 m and the vapour pressure deficit were estimated from other parameters (see Appendix B, Eq. B.1 and B.2). Daily global radiation was provided by the World Radiation Data Centre (WRDC). This parameter is barely measured in the weather stations of Siberia. Thus, we used the data from the station of Omsk (latitude 54.56 ° N, longitude 73.24 ° E, elevation 94 m), which is located 680 and 739 km away from the weather stations of BAR (latitude 53.40 ° N, longitude 83.50 ° E, elevation 183 m) and TOM (latitude 56.50 ° N, longitude 84.92 ° E, elevation 141 m), respectively. Simple gap-filling procedures were applied when necessary (Appendix B).

In Siberia, the soil is covered every winter by a continuous snow cover. Typically, for our study sites, a continuous and seasonally permanent snow-pack sets up in November and disappears in March–April. This snow-pack influences soil water dynamics and has to be taken into account when modelling soil water budgets. It is not possible to explicitly implement snow cover effects in Biljou. To do this, we modified the precipitation input of the model in such a way that no water could penetrate into the soil when a continuous and seasonally permanent snow-pack

was present on its surface until the period of snow-melt. At snow-melt, all the water contained in the snow-pack (i.e. the sum of winter precipitations) was released (Appendix B).

Finally, we constructed for each study site a set of complete climate series spanning the period 1966–2015.

Soil and vegetation characteristics

On each site and under each vegetation cover, we defined four soil layers down to 120 cm. These four layers fitted with the pedological horizons and soil physico-chemical properties described on three replicate pits in July 2013 (see Brédoire et al. 2016a; Brédoire et al. 2016b).

The proportion of fine roots in each soil layer was derived from the β values reported by (Brédoire et al. 2016b). Since soil physico-chemical properties were measured on the depths −5, −15, −30, −60, and −100 cm, we estimated their values for the four soil layers by weighted means. We estimated the water content at the field capacity and the water content at the wilting point using the pedo-transfer functions of the R package *euptf* version 1.2 (Tóth et al. 2015).

Leaf area index (LAI) was estimated by collecting litterfall in autumn 2013. Five litter-traps of 1.96 m^2 each were set up earlier in the season on each site. We sorted the litterfall to keep only the leaves and oven dried them at 60 °C until constant weight. For each site, the surface area and the dry weight of 20 leaves was then used to compute LAI in m^2 leaves m^{-2} ground.

Calibration of the model

Biljou provides the extractable water content (W, in mm) for each of the four soil layers implemented. We converted W to total volumetric water content (VWC, in m^3 water m^{-3} soil) at the day d as following:

$$\mathrm{VWC}_d = 10 \times \frac{\mathrm{W}_d - \mathrm{W}_{d-1}}{h} + \mathrm{VWC}_{d-1} \tag{4.5}$$

where h is the thickness of the layer (in cm). The value of VWC_0 was empirically determined in order to obtain the best fit with field measurements.

The calibration of the model consisted in the empirical determination of the best values for the phenological dates (budburst and leaves abscission) as well as for soil micro- and macro-porosity. The manipulation of the soil porosity in the model influences preferential water flow in the soil profile, i.e. the proportions of water refilling the water reserve and of water drained. The quality of the fit was graphically checked (VWC simulated over time along with VWC measured). We also computed different errors (residuals, absolute error and relative error) which had to be as low

Table 4.1: Description of the Biljou simulations under modified climatic conditions. All the simulations were conducted over 1966–2012.

Run	Description
Control	Simulation under actual site conditions
Run 1	Weather data imported from another station with drier conditions
Run 2	Same as Run 1 but keeping the winter precipitations of the Control
Run 3	Same as Run 2 but multiplying winter precipitations by 1.5
Run 4.1	Same as Run 1 but adding 15 days at the beginning and 15 days at the end of the vegetation season
Run 4.2	Same as Run 2 but adding 15 days at the beginning and 15 days at the end of the vegetation season
Run 4.3	Same as Run 3 but adding 15 days at the beginning and 15 days at the end of the vegetation season

as possible. We assumed the two layers not equipped with soil moisture sensors in the field had similar properties to adjacent layers. The calibration was done over the period of field measurements, i.e. May 2013–October 2015.

Soil water budget under different climatic scenarii

We performed two types of simulation: (1) under actual site conditions for the whole period of qualitative climate monitoring in SW Siberia (i.e. 1966–2015), and (2) under modified climatic conditions.

The purpose of the first type of simulation was to characterize the soil water dynamics of our experimental sites in the last decades. More precisely, we wanted to identify: (1) the dynamics of soil water content over seasons, (2) the key periods controlling these dynamics ("hot moments"), and (3) extreme or rare events, their intensity and their frequency.

The objective of the second type of simulation was to characterize the impact of changing temperature and precipitation on the water budget. Because we did not have access to climate projections for SW Siberia on a daily time step and at local spatial scale, we used, for a given site, the climate data of a weather station with higher mean annual temperature and lower precipitation. Concretely, we used the climate data from Barnaul (BAR) at TOM and from Slavgorod[1] at BAR. Such a switch of climatic conditions has the advantage to provide realistic combinations of all the climate variables required for the model. In addition, simulating the water budget over 42 years (1966–2012), we approached the natural range of variations of these combinations.

1. Slavgorod is the weather station we used for the site KRA, see the other Chapters.

4.3 Results

4.3.1 Monitoring of the soil temperature and moisture

The soil temperature measured in the field presented some spatial variability at wintertime (up to about 3 °C difference between 2 replicates per condition at BAR forest in the winter 2013–2014) but almost no variability in the rest of the year (Fig. 4.1 to 4.4).

The soil volumetric water content (VWC) measured in the field varied on the site scale—between the soil pits equipped with sensors—and somewhat on the pit scale—between the different sensors in a soil pit—(Fig. B.3 to B.6). These variabilities tended to be the same over seasons. In the following analysis, we averaged, for each depth, the soil VWC measured in each pit (n = 2–3 sensors per pit) and then per snow treatment (n = 2 pits).

At BAR, the soil VWC reported by the sensors abruptly dropped down at the beginning of winter and was maintained at low values until the snow-melt (Fig. B.3 and B.4). This phenomenon was probably an artefact related to the range of temperatures the sensors are calibrated to make accurate measurements. In fact, these soil VWC drops were reported when the soil temperature was < 0 °C and were less important and less frequent at TOM, where the soil temperature barely went below this threshold (Fig. 4.1 to 4.4).

In all experimental plots, over the vegetation season, the soil temperature followed the variations of the air temperature (see the "control" on Fig. 4.1 to 4.4). In winter, the soil temperature varied only a little while air temperature experienced the biggest amplitude of its variations. The amplitude of variation of the soil temperature decreased with soil depth. On average, the air temperature was warmer at BAR than at TOM. This was also the case for soil temperature, except during the winter, where the inverse trend was observed. Except in winter, where differences were rather small, the soil temperature was higher in grassland than in forest. Typically, the air temperature increased from the middle of winter (the minimum daily averages, below −25 °C, were reported in January–February) to the middle of summer (maximum daily averages, around 25 °C, in July) and decreased from the middle of summer to the middle of winter. The soil temperature raised from the moment where the snow-pack disappeared (in winter, soil temperature was maintained close to 0 °C) to the middle of summer (up to about 25 °C at BAR grassland, and to 20 °C at TOM grassland). Soil thermal inertia was illustrated by the delay of soil temperature responses to the variations in air temperature with depth.

On average, the soil VWC was set at its maximum at the end of the snow season and decreased over the vegetation season (Fig. 4.1 to 4.4). Punctual recharges occurred at spring and summer, corresponding to precipitation episodes, which were of greater intensity in summer. In autumn, the soil VWC was almost back to its

maximum at TOM. The dynamics of soil VWC were very similar between forest and grassland but differed between the two sites. Generally, the soil at BAR tended to be drier than at TOM.

4.3.2 Snow manipulation experiment

For each site, the control plot and the increased snow plot were spatially close, thus we assume there was no difference in weather and soil conditions. This is in agreement with air temperature recordings (Fig. 4.1 to 4.4).

Barnaul

At BAR forest, all snow applications permitted to increase the height of the snow cover: about +38 cm in winter 2013–2014, and +25 cm in 2014–2015 (Fig. 4.1). The two snow conditions started to melt simultaneously but the treatment ended to melt about 10–13 days later. At BAR grassland, the increase of snow height induced by the treatment was not perfectly maintained in the winter 2013–2014 (approximately +13 cm but part of the treatment plot presented similar levels as in the control), possibly due to wind blowing (Fig. 4.2). In 2014–2015, the treatment was better maintained and permitted an increase of 25 cm. In grassland, the end of snow-melt occurred almost the same day in the two snow conditions in both years.

At BAR, the snow season began late in the winter 2013–2014, the snow height remained low in natural conditions (Fig. 4.1 and 4.2). The soil was frozen, at least until −15 cm, when the snow-pack settles and the depth of freezing continued to increase since negative temperatures were recorded later at −60 cm in the two snow conditions in forest and in grassland. As such, soil moisture recordings were not accurate during this winter. In forest, soil temperature at the three depths studied was lower in the control than in the increased snow treatment (up to 2.5 °C difference in winter 2013–2014; Fig. 4.1). No clear differences in soil temperature were observed in grassland, the control tended to be slightly warmer than the treatment (up to 1.5 °C difference in winter 2013–2014; Fig. 4.2). This has certainly to be related to the relative inefficiency of the snow addition at BAR grassland in the winter 2013–2014. In the winter 2014–2015, the snow-pack settles on unfrozen soil at BAR forest and grassland (Fig. 4.1 and 4.2). The snow treatment prevented soil freezing in forest but not in grassland where soil slightly frost under both snow conditions. At the period of snow-melt, for the two winters studied, the soil temperature tended to rise 5–10 days earlier in the control than in the treatment (Fig. 4.1 and 4.2). In the increased snow treatment, the peak of soil VWC tended to be higher and to occur a few days later than in the control. However, we note that at BAR forest −60 cm and BAR grassland −15 cm, the average soil VWC was often higher in the control than in the treatment, and this before the beginning of snow manipulations (Fig. 4.1 and

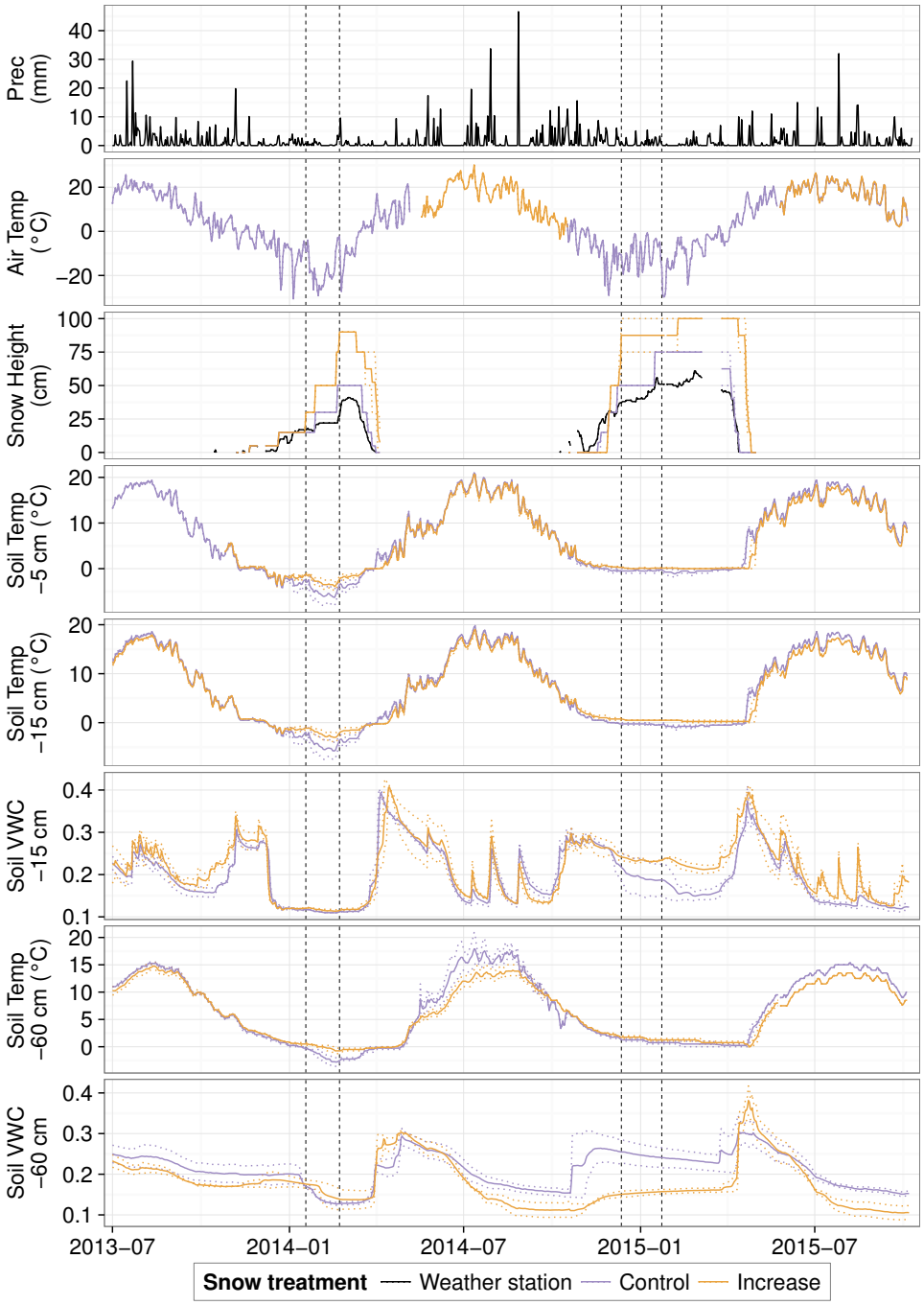


Figure 4.1: Impacts of the snow manipulation on the soil physical status at BAR aspen forest. Soil status monitoring data (temperature and volumetric water content, VWC) are shown along with precipitation at the weather station, and temperature and snow height at the experimental site. The vertical lines shows the dates of snow manipulation (snow application in the "increased" treatment). All results are daily averaged values (n = 1–2), the dotted lines show daily averaged minimum and maximum.

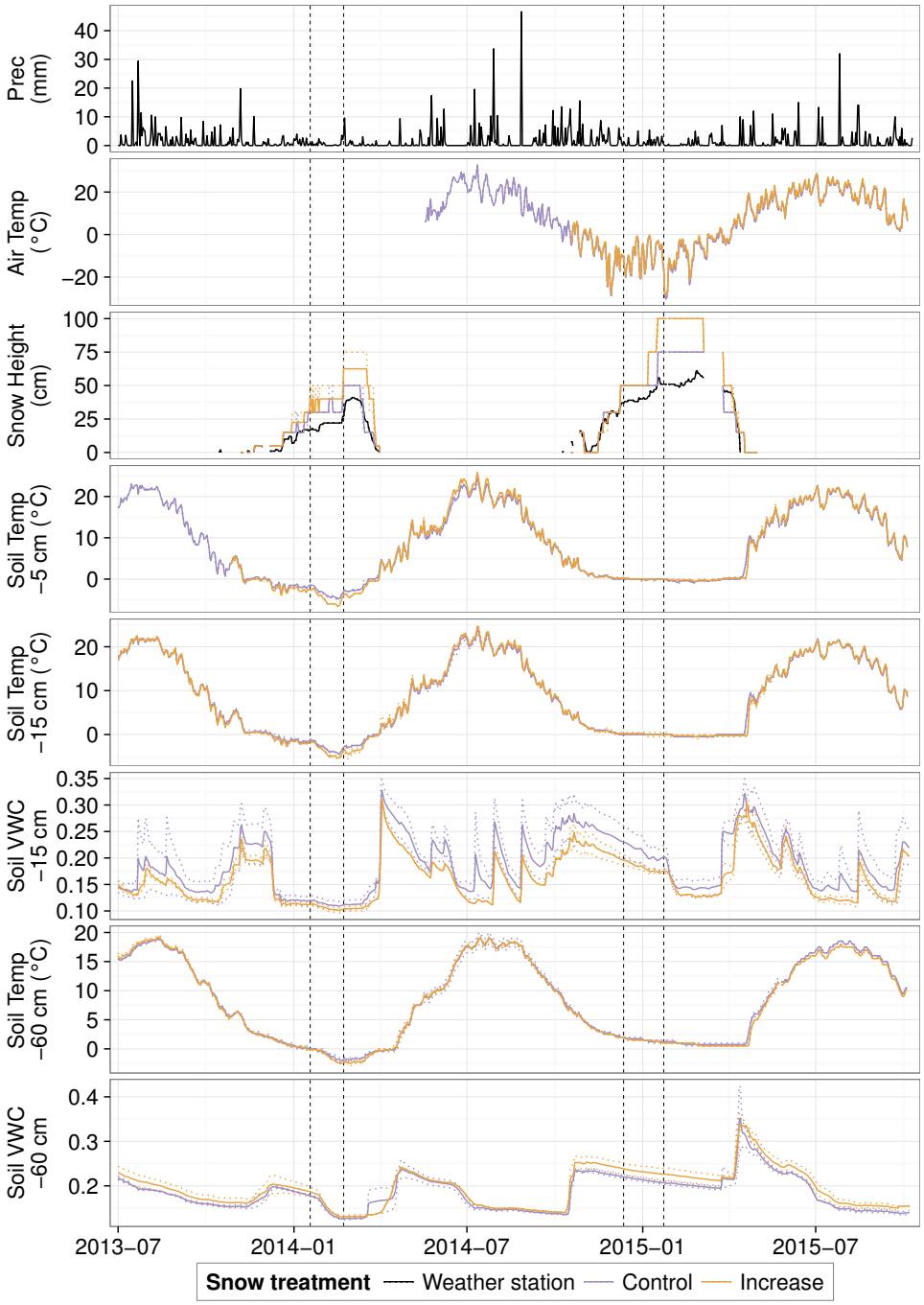


Figure 4.2: Impacts of the snow manipulation on the soil physical status at BAR grassland. Soil status monitoring data (temperature and volumetric water content, VWC) are shown along with precipitation at the weather station, and temperature and snow height at the experimental site. The vertical lines shows the dates of snow manipulation (snow application in the "increased" treatment). All results are daily averaged values (n = 1–2), the dotted lines show daily averaged minimum and maximum.

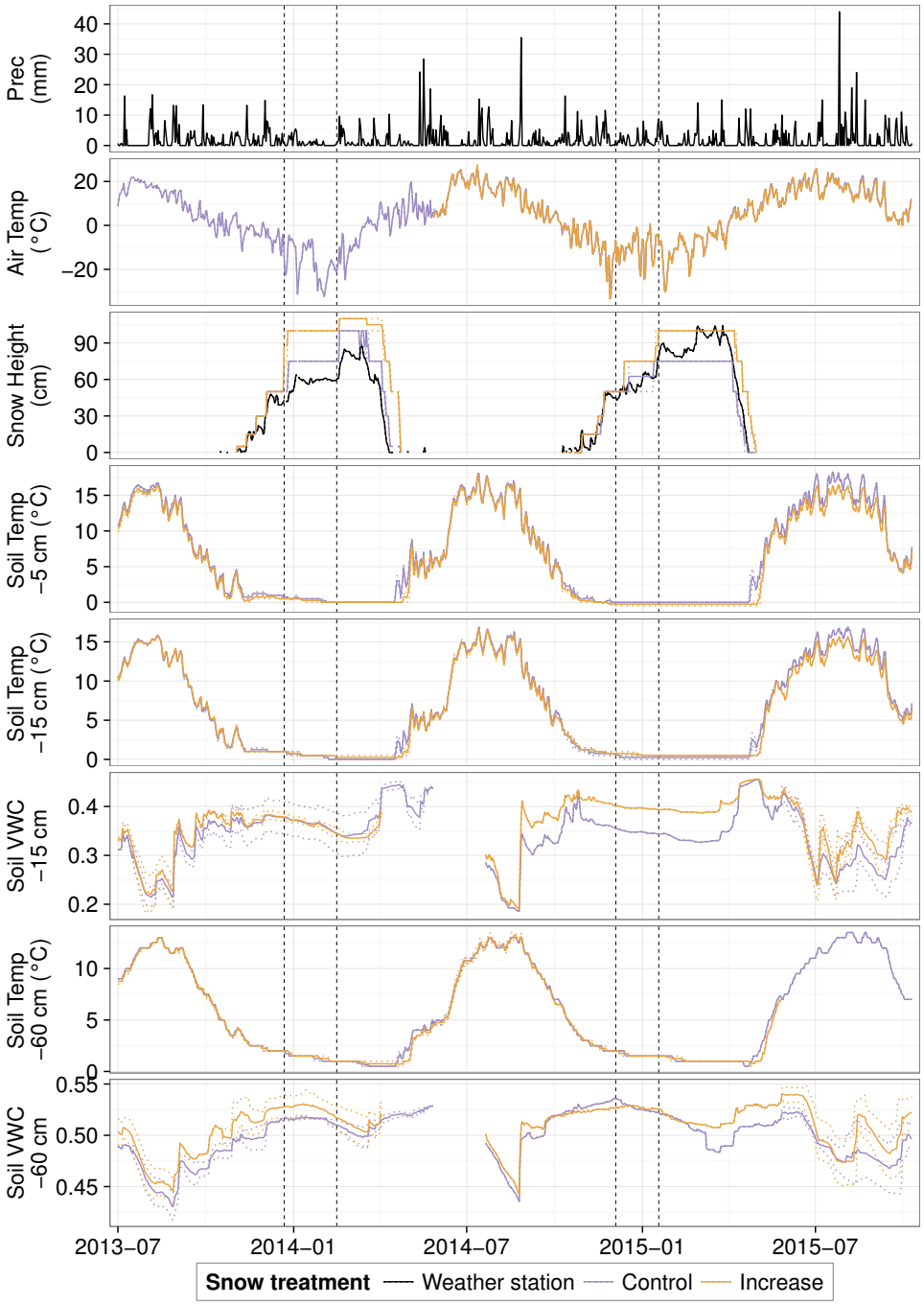


Figure 4.3: Impacts of the snow manipulation on the soil physical status at TOM aspen forest. Soil status monitoring data (temperature and volumetric water content, VWC) are shown along with precipitation at the weather station, and temperature and snow height at the experimental site. The vertical lines shows the dates of snow manipulation (snow application in the "increased" treatment). All results are daily averaged values (n = 1–2), the dotted lines show daily averaged minimum and maximum.

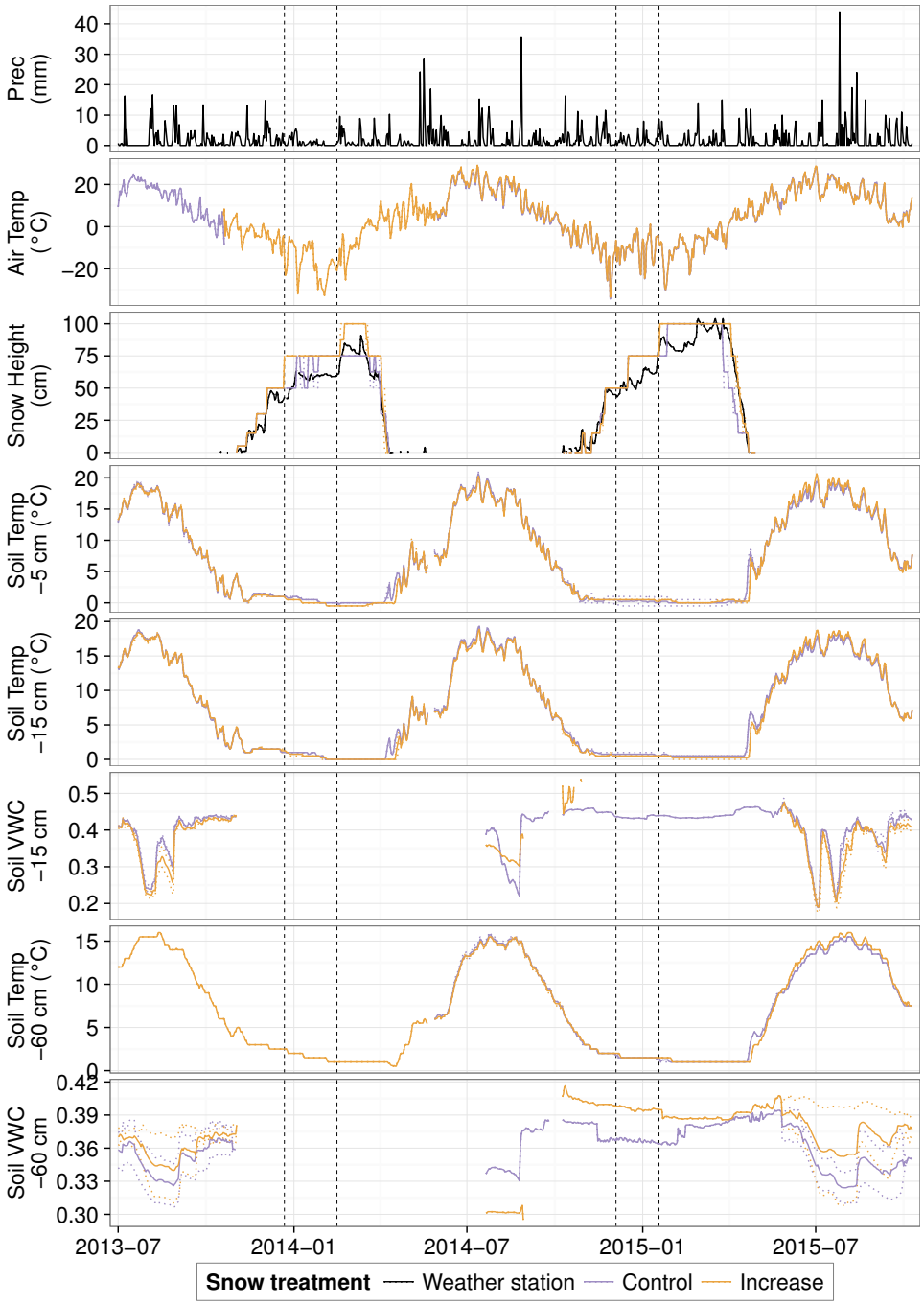


Figure 4.4: Impacts of the snow manipulation on the soil physical status at TOM grassland. Soil status monitoring data (temperature and volumetric water content, VWC) are shown along with precipitation at the weather station, and temperature and snow height at the experimental site. The vertical lines shows the dates of snow manipulation (snow application in the "increased" treatment). All results are daily averaged values (n = 1–2), the dotted lines show daily averaged minimum and maximum.

4.2). This could be attributed to spatial variability in micro-topography and/or soil physico-chemical properties (e.g.: gentle slope, soil density/porosity, clay content).

Tomsk

At TOM forest, the snow applications increased the snow height by 25 and 10 cm (respectively after the first and the second application) in the winter 2013–2014, and by 25 cm in 2014–2015 (Fig. 4.3). At TOM grassland, the snow height was increased by 25 cm the first winter (Fig. 4.4). In the second winter, the last application also permitted to increase the snow height by 25 cm but a snowfall event, a few days later, raised the control to 1 m. Since we did not set up temperature sensors above 1 m, we were not able to know if there were different snow heights in the two treatments for the rest of the snow season (Fig. 4.4) As for BAR, the snow-melt at TOM forest started simultaneously in the two snow conditions but ended about 10 days later in the increased snow treatment. In grassland, the snow-melt ended almost the same day.

Over the period of monitoring, the seasonally permanent snow cover never settles on frozen soil at TOM forest and grassland (Fig. 4.3 and 4.4). Temperatures as low as −0.5 °C (average minimum) were sometimes recorded at −5 cm. No clear differences in soil temperature were observed between the two snow conditions until the snow-melt, where the temperature rise occurred about 10–15 days earlier in the control than in the treatment in both forest and grassland.

At TOM, the soil was saturated with water at snow-melt in the control. Soil surface runoff was observed on the experimental field site. We lost, by immersion of electronics, many data loggers for the soil VWC sensors at this period (!). As a consequence, we only have an accurate recording of soil VWC at the period of snow-melt for TOM forest in 2015. For this recording, we observed a peak of soil VWC right after the snow-melt but no difference between the two snow conditions at −15 cm, and higher VWC under the increased snow treatment at −60 cm (Fig. 4.3). However, we note that the average VWC at −60 cm was most of the time higher in the area of the increased snow treatment (even before we started the experiment).

4.3.3 Calibration of the soil water budget model

The calibration of the soil water budget model Biljou was performed on the period of available field measurements (2013–2015). The resulting values of the input parameters are presented in Table 4.2. The best fits of soil volumetric water content (VWC) computed with the model are presented in the Fig. 4.5, 4.6, B.7, and B.8. Due to the short period of field monitoring, we were not able to perform an accurate verification of our calibrations on independent time series.

Table 4.2: Input parameters of the soil water budget model BILJOU for our study sites of BAR and TOM in aspen forest (FOR) and in grassland (GRA).

Site	Veg.	Input parameters							
		Vegetation parameters							
		Budburst[c]	Fall[c]	LAI_{max}[ac]					
BAR	FOR	122	288	4.94					
	GRA	110	288	6.00					
TOM	FOR	157	280	3.90					
	GRA	155	288	5.00					
		Soil parameters							
		Depth	Roots[a]	W_{FC}[b]	W_{WP}[b]	AD[a]	RD[b]	ah[c]	bh[c]
BAR	FOR	23	39	41.68	0.16	1.13	2.4	0	1.65
		49	28	44.77	0.15	1.21	2.4	0	1.65
		85	21	53.05	0.15	1.28	2.5	0	1.70
		120	12	41.70	0.13	1.44	2.5	0	1.70
	GRA	23	59	39.79	0.15	1.20	2.4	0	1.60
		47	26	40.29	0.14	1.27	2.4	0	1.65
		84	13	50.05	0.11	1.66	2.5	0	1.80
		120	2	41.68	0.11	1.65	2.5	0	1.80
TOM	FOR	20	65	39.44	0.16	1.02	2.4	0	1.30
		49	22	56.17	0.12	1.23	2.4	0	1.50
		74	12	28.10	0.15	1.47	2.5	0	1.55
		120	1	28.38	0.19	1.45	2.5	0	1.55
	GRA	20	75	43.00	0.14	1.08	2.4	0	1.30
		53	17	33.92	0.12	1.33	2.4	0	1.50
		75	7	33.93	0.17	1.52	2.5	0	1.55
		120	1	33.61	0.19	1.42	2.5	0	1.55

Budburst: day of leaf apparition (julian day); Fall: day of leaf abscission (julian day);
LAI_{max}: maximum leaf area index; Depth: depth of the bottom of the soil layer (cm);
Roots: fine root proportion (%); W_{FC}: water content at the field capacity (mm);
W_{WP}: water content at the wilting point (g water g^{-1} soil); AD: apparent density; RD: real density;
ah bh: micro- and macro-porosity (the latter controls preferential flow)
[a] measured; [b] estimated; [c] fitted

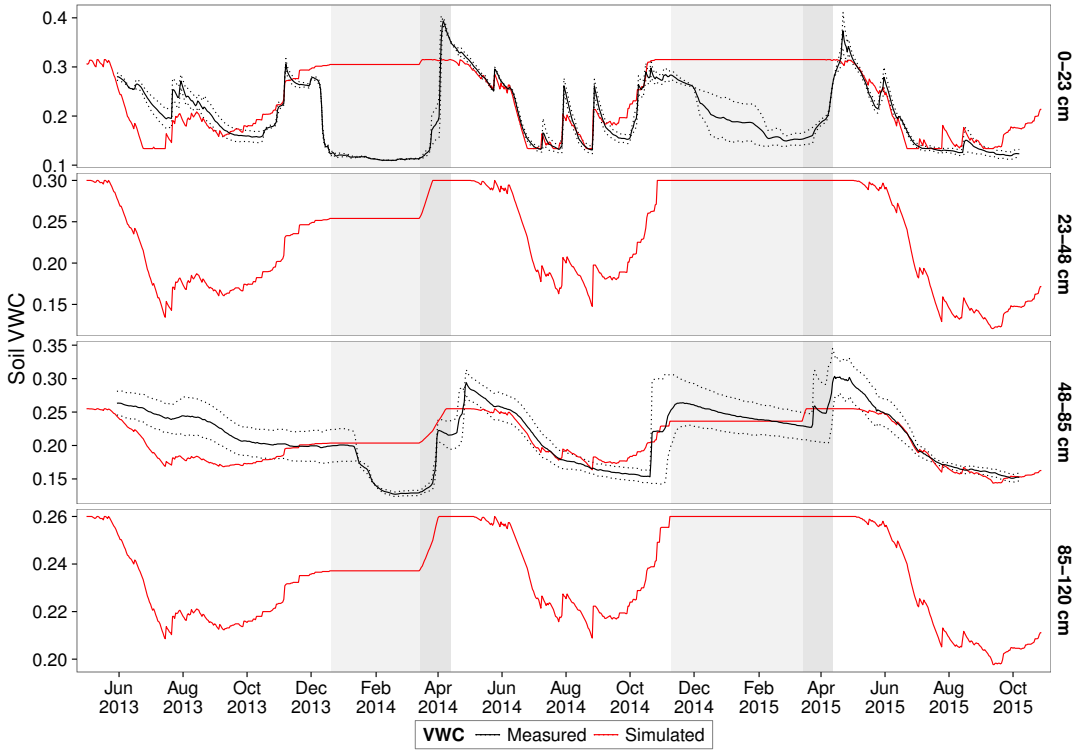


Figure 4.5: Calibration of the soil water budget model BILJOU at BAR forest. Volumetric water content (VWC, in m^3 water m^{-3} soil) in four soil layers: simulations (red lines) and field measurements (black lines) over the period of VWC monitoring. The black dotted lines indicate the minimum and the maximum of the mean VWC (mean of 2–3 sensors per depth and per pit) measured on 1–2 plots. The snow season is highlighted in grey and the snow-melt in dark grey. In winter, when the soil temperature is close to or below 0 °C, the soil moisture sensors do not always provide accurate data.

The VWC computed with the model was in good agreement with field measurements at both BAR aspen forest and grassland (Fig. 4.5, B.7, and B.9). The root mean square errors (RMSE), excluding winter and measurements at temperature < 0 °C, ranged between 0.023 and 0.034.

At TOM aspen forest and grassland, the model simulated well the VWC in the upper soil layer (RMSE, excluding winter and measurements at temperature < 0 °C: 0.041–0.057) but the simulation was not as good in the deeper layer (RMSE, excluding winter and measurements at temperature < 0 °C: 0.024, Fig. 4.6, B.8, and B.9). In particular, the model did not reproduce the abrupt refilling of the soil water reserve observed at −60 cm at the end of the summer 2014 (Fig. 4.6 and B.8). This can probably be attributed to a variation of the climatic conditions between the experimental sites and the weather station from which we get the data. In fact,

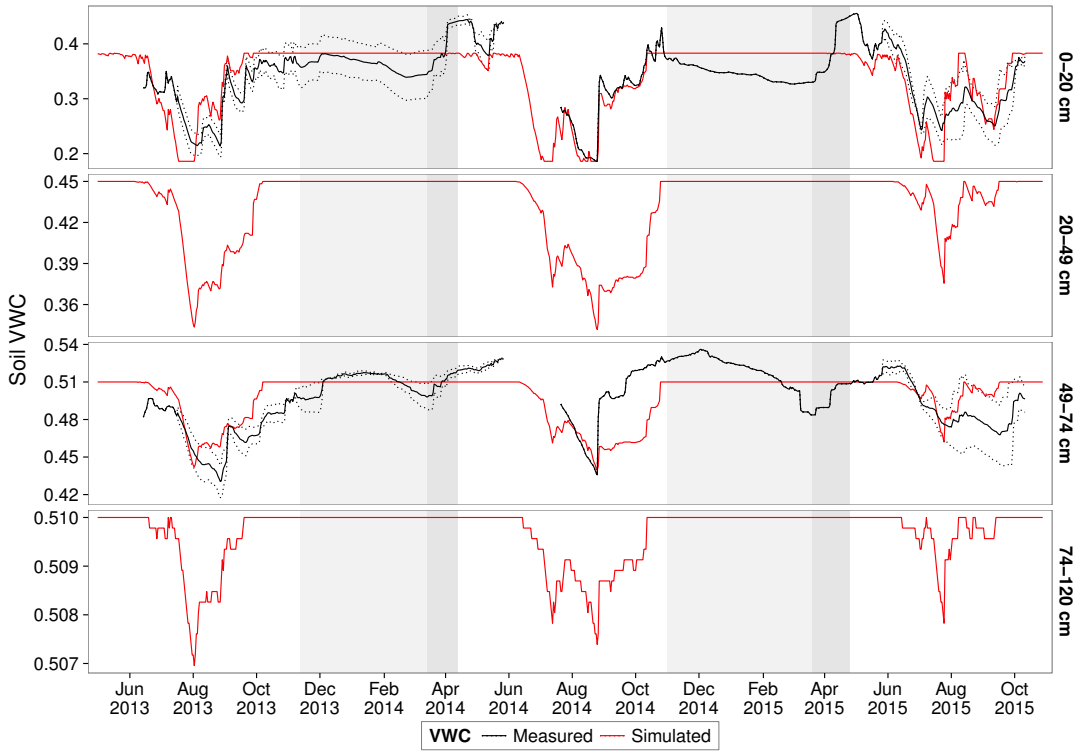


Figure 4.6: Calibration of the soil water budget model BILJOU at TOM forest. Volumetric water content (VWC, in m^3 water m^{-3} soil) in four soil layers: simulations (red lines) and field measurements (black lines) over the period of VWC monitoring. The black dotted lines indicate the minimum and the maximum of the mean VWC (mean of 2–3 sensors per depth and per pit) measured on 1–2 plots. The snow season is highlighted in grey and the snow-melt in dark grey. In winter, when the soil temperature is close to or below 0 °C, the soil moisture sensors do not always provide accurate data.

adding 30 mm of precipitation on 26/08/2014—i.e. simulating a local intense summer rainfall event—permitted to better reproduce the VWC dynamics measured at this period under both vegetation covers (data not shown).

The soil VWC measured at the period of snow-melt, or soon after, tended to be higher than the VWC simulated. This phenomenon was due to the high input of water at this moment, the sensors indicating a peak of VWC between the field capacity and the saturation while the model BILJOU is limited to the water content at the field capacity.

4.3.4 Soil water budget simulations

Soil water budget simulations over the last decades

At BAR forest, the peak of incident rainfall simulated occurred typically at the snow-melt (about 110 mm on average, distributed between the end of April and the beginning of May) and permitted a recharge of the soil REW (see "control" on Fig. 4.7). Over the rest of the vegetation season, the average sum of precipitations per 15 days was about 20 mm with a peak at 40 mm in the second half of July. On average, the REW simulated started to decrease from the beginning of May until the beginning of September (0.30). It fell below the threshold of 0.4 in July. However, due to the inter-annual variability, the average number of stress days started to be > 0 from the beginning of May, it reached as high as 12 days of stress per 15 days in August. This high average number of stress days indicates that stress occurs in summer in most of the years (Fig. B.10). On average, 75 days of stress (min–max: 0–75, confidence interval at 95 %: 11) and a stress intensity (I_s) of 32 (0–74, 7) were simulated at BAR forest. On average, the stress simulated started at the day 190 (149–251, 7). Drainage occurred almost exclusively at the period of snow-melt, at spring. It peaked at about 16 mm in the first 15 days of April and gradually decreased until the beginning of June, from which it would not exceed 2 mm per 15 days until the following snow-melt (Fig. 4.7). The average cumulative drainage simulated over the year at BAR forest was 56 mm (13–56 mm, confidence interval at 95 %: 12 mm).

At TOM forest, the peak of the incident rainfall simulated also occurred at the snow-melt, reaching about 90 mm per 15 days at the beginning of April (see "control" on Fig. 4.8). The average incident rainfall simulated then decreased to 24 mm at the beginning of May and varied between 25 and 40 mm during the vegetation season. On average, the REW simulated was set at 1 at the beginning of April (snow-melt) and decreased to 0.65 between June and August. From the beginning of September, the average REW started to rise until 0.9. The average REW simulated at TOM forest never reached the threshold of 0.4 and the average number of stress days varied from 1 to 2.5 between July and September (4.8). In fact, stress conditions did not occur every year at this site (Fig. B.10), we simulated 0–77 days of stress per vegetation season (mean: 6, confidence interval at 95 %: 6) and a stress intensity of 0–36 (2, 2). On average, the stress simulated started at the day 219 (200–256, 9). The average drainage simulated peaked at 75 mm in the first 15 days of April (snow-melt) and was never above 15 mm after the beginning of June (4.8). The average annual drainage simulated was 255 mm (min–max: 122–388 mm, confidence interval at 95 %: 20 mm).

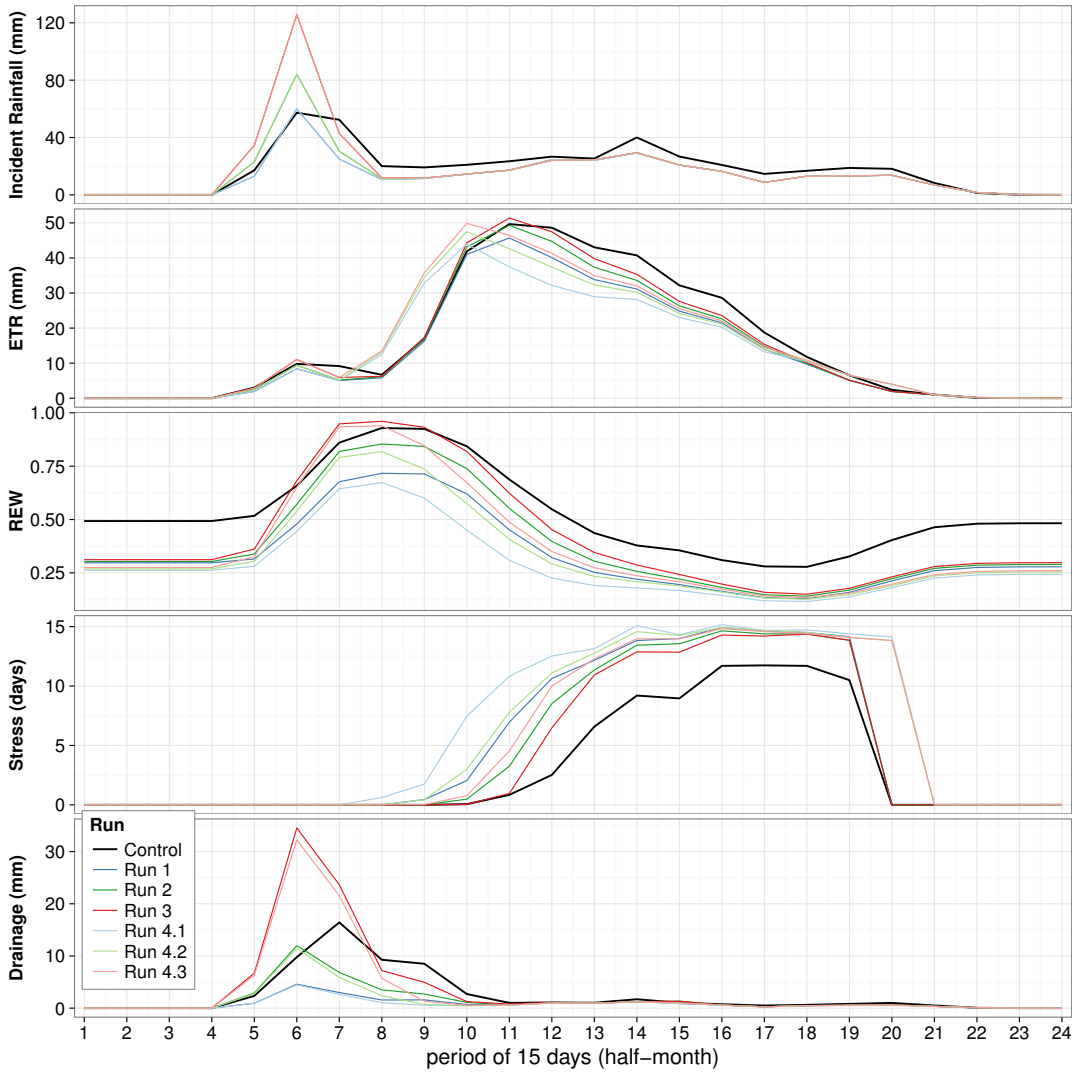


Figure 4.7: Water budget simulations at BAR forest averaged on a half-month time step for the period 1966–2012. For each year, daily incident rainfall, evapo-transpiration (ETR), stress and drainage were summed while daily relative extractable water content (REW) was averaged over the 15 days time step. The runs are described in Table 4.1.

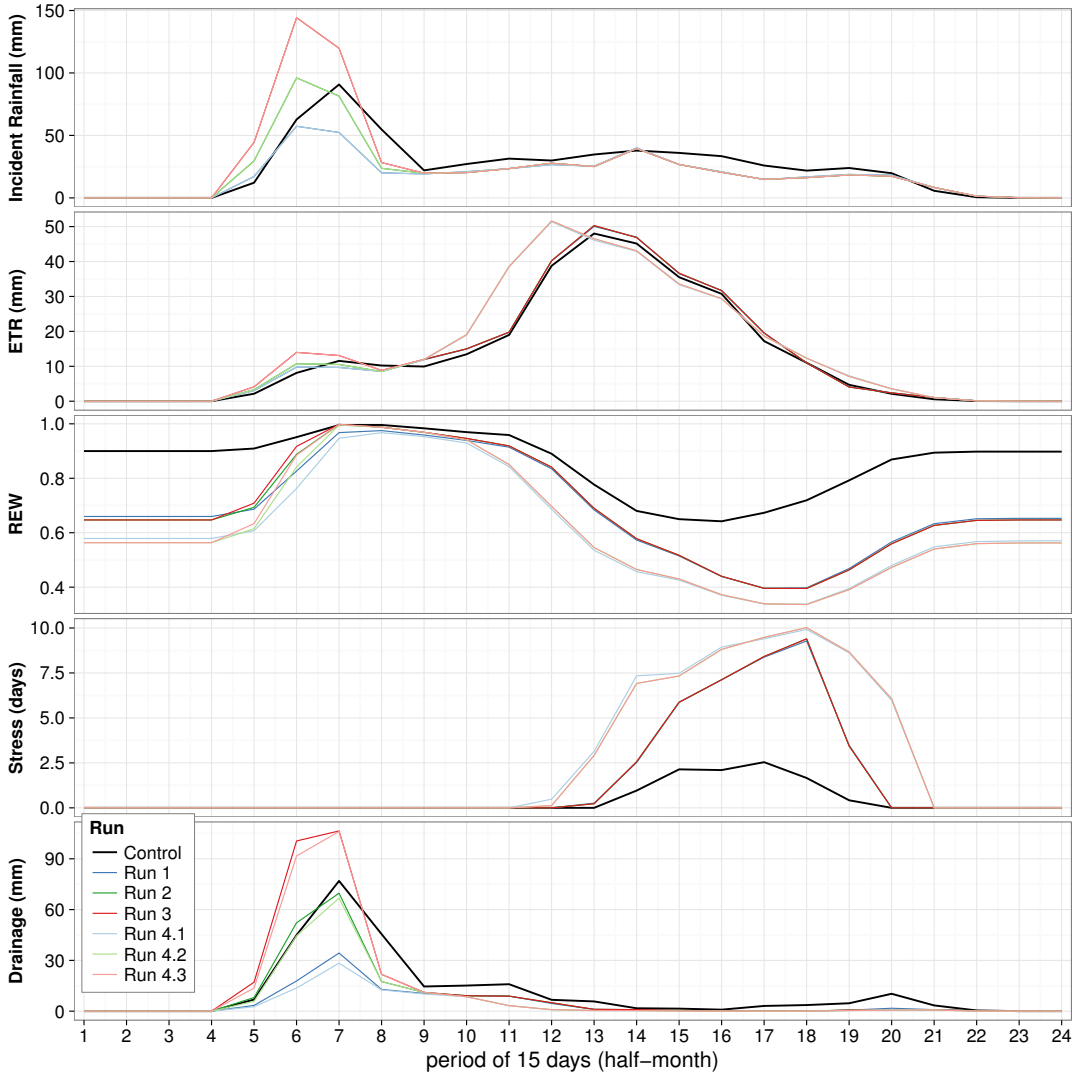


Figure 4.8: Water budget simulations at TOM forest averaged on a half-month time step for the period 1966–2012. For each year, daily incident rainfall, evapo-transpiration (ETR), stress and drainage were summed while daily relative extractable water content (REW) was averaged over the 15 days time step. The runs are described in Table 4.1.

Soil water budget simulations under modified climatic conditions

At BAR forest, the modifications of the climatic conditions (runs 1 to 3), eventually coupled with an increase of the length of the vegetation season (runs 4.1 to 4.3; see Table 4.1 for details on the runs), mainly impacted the amount of incident rainfall at the period of snow-melt (+3, +27 and +68 mm, as compared to the control, for the runs 1, 2 and 3, respectively) while, over the rest of the vegetation season, all simulations (runs 1–4.3) had the same precipitations, about −1 to −10 mm per 15 days in comparison with the control (Fig. 4.7). On average, the runs 1 (and 4.1), 2 (and 4.2) and 3 (and 4.3) had an annual incident rainfall of 324, 463 and 428 mm, respectively, against 423 mm for the control (Fig. 4.9). All the runs led to a mean REW over the vegetation season lower than the control (0.27–0.40 against 0.48 for the control), the lowest being for the run 4.1 (Fig. 4.9). The difference in the average REW between the runs seems to be mainly attributable to a different recharge of the soil plant extractable water (W) reserve at snow-melt (Fig. 4.7). All runs led to an earlier apparition of stress (10–42 days earlier, on average), as well as longer (26–74 days more) and more intense stress conditions (22–60 stress intensity units more) than the control (Fig. 4.7 and 4.9). The earlier beginning of the vegetation season in the runs 4.1–4.3 contributed to an earlier discharge of the water reserve and an earlier apparition of stress (13–15 days before), in comparison with the runs 1–3 (Fig. 4.7 and 4.9). The average yearly drainage simulated varied from 31 (run 4.1) to 151 % (run 3) of the control (Fig. 4.9). Only the runs 3 and 4.3—the runs with 1.5 times the actual snow cover of the site—led to a higher annual average drainage than in the control. The runs 2 and 4.2 did not permit a similar drainage to the control despite the same amount of water released at snow-melt (Fig. 4.7). This has to be related to the level of REW at the beginning of the preceding winter: since the REW at this moment was lower in the runs 2 and 4.2 than in the control, a greater part of the water issued from the snow-melt was captured by the soil (filling of the water capacity) and the drainage was lower in the runs 2 and 4.2 (Fig. 4.7). For all the runs, the average peak of drainage occurred one period (half-month) earlier than for the control. On average, the earlier the vegetation season started, the lower the drainage was. However, the average differences between the runs 1–3 and 4.1–4.3 were only of 2–11 mm, respectively.

At TOM forest, the modification of the climatic conditions (see the runs 1 to 3, and 4.1 to 4.3 for a coupling with a lengthening of the vegetation season; Table 4.1) also impacted the incident rainfall, mostly at the period of snow-melt (Fig. 4.8). All the simulations with modified climatic conditions peaked in the 15-days period preceding the control. While the control peaked at about 90 mm of incident rainfall per 15 days, the runs 1 (and 4.1), 2 (and 4.2) and 3 (and 4.3) peaked at 55, 95 and 145 mm, respectively (Fig. 4.8). From the beginning of April to the end of the vegetation season, the incident rainfalls of the runs 1–4.3 were a few mm below the control (ex-

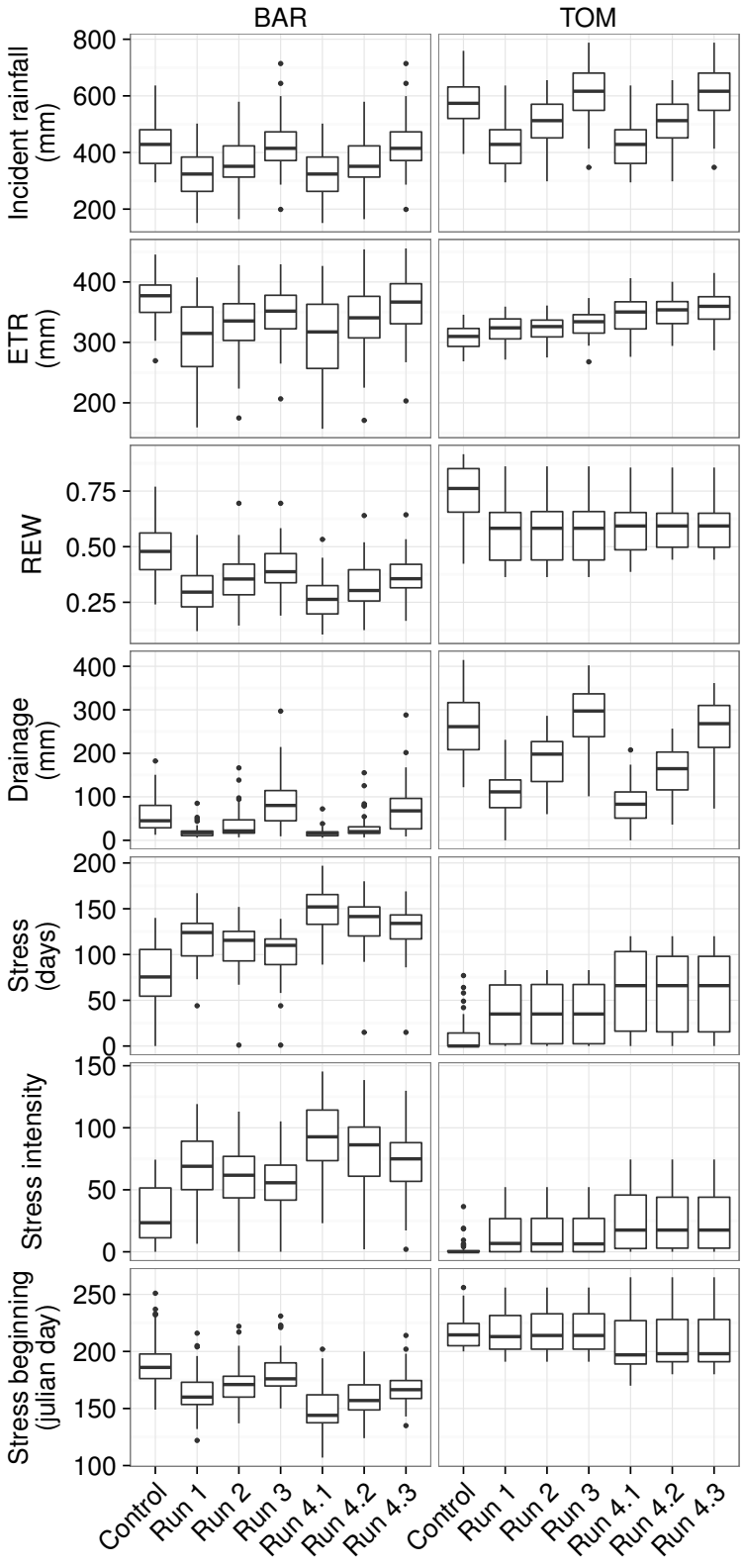


Figure 4.9: Synthesis of the water budget simulations over the period 1966–2012. Daily incident rainfall, evapo-transpiration (ETR), and drainage were yearly summed. Relative extractable water content (REW) was averaged yearly over the vegetation season. The stress indexes were computed yearly over the vegetation season. The runs are described in Table 4.1.

cept at the beginning of July). Consequently, the differences in the incident rainfall levels observed at snow-melt were found back on the yearly trends (423, 507 and 613 mm for the runs 1, 2 and 3, respectively, against 563 for the control; Fig. 4.9). The REW averaged over the vegetation season was lower for all the runs than for the control. The runs 1–3 on one hand, and 4.1–4.3 on the other hand, presented the same patterns (Fig. 4.8 and 4.9). All simulations under modified climatic conditions led to an earlier and a longer decrease of REW and this decrease was stronger when the vegetation season was longer. While the average minimum REW simulated for the control (about 0.65) was reached in the first 15 days of August, the runs 1–3 reached 0.40 and the runs 4.1–4.3 0.35, both in September (Fig. 4.8). The simulations under modified climatic conditions induced more frequent and more intense (average stress intensity was 13–26 against 2 for the control) stress conditions (Fig. 4.8, 4.9 and B.10). The longer vegetation season exacerbated this phenomenon and lengthened the period of stress: the stress started one period (15 days) before and ended one period later in the runs 4.1–4.3 than in the runs 1–3 (Fig. 4.8). As observed at BAR, the increase in average incident rainfall did not conducted to higher drainage levels in the simulations. In fact, the average yearly drainage simulated were 104, 186 and 284 mm for the runs 1, 2 and 3 respectively, against 255 mm for the control. The drainages of the runs 4.1–4.3 were about 25 mm lower than for the runs 1–3. Again, most of the drainage occurred at snow-melt (up to 110 mm in 15 days for the runs 3 and 4.3). All the peaks of drainage simulated at TOM forest occurred at the beginning of April (Fig. 4.8).

4.4 Discussion

4.4.1 Characterization of the soil temperature and water dynamics over seasons

Monitoring and simulations

On average, BAR experienced drier climatic conditions than TOM over the period of monitoring on our field sites (2013–2015; compare the “control” on the Fig. 4.1 to 4.4). Similar trends were simulated for the period 1966–2012 (see the “control” on the Fig. 4.7, 4.8, 4.9 and B.10). BAR had lower relative extractable water content (REW) in the vegetation season and experienced regular (almost every year) stress conditions (i.e. REW < 0.4) which were both longer and more intense than at TOM. At TOM, stress conditions occurred on an irregular basis, they generally appeared late in the vegetation season and thus stand for a relatively short period. BAR typically experienced colder soil conditions in winter but warmer in the rest of the year than TOM. These differences between BAR and TOM have to be related to the different

climatic conditions of the two sites. Mainly, BAR had higher air temperature, lower rainfall (thus lower incident rainfall), later snow-pack establishment in the season and lower snow height than TOM. In addition to climatic conditions, differing soil properties—such as density, porosity, particle size distribution, mineralogical composition, organic matter composition, size of aggregates, etc.—as well as different vegetation communities—understorey in forest and grass species in grassland—have an impact on soil temperature and water dynamics. This was evidenced by the simple climate switch at TOM (run 1): implementing the climate of BAR led to very different soil water dynamics. However, the effects of soil and vegetation were not directly tested in the framework of this study.

The simulations of the water budget under modified climatic conditions essentially consisted in applying drier climate during the vegetation season, testing different levels of snow in winter, and testing the effect of a lengthening of the vegetation season (Table 4.1). The drier conditions induced a greater depletion of the REW in both sites (Fig. 4.7, 4.8, 4.9 and B.10). Overall, the severity of the depletion was modulated by the length of the vegetation season: the longer the season was, the greater was the depletion. This was particularly the case at TOM since at BAR the REW simulated was already very close to its minimum in the less severe scenario (i.e. the run 3). The variations in snow levels only had a marginal effect on the minimum REW at BAR and did not impact the minimum REW at TOM (compare the runs 1–3). However, all simulations conducted to an earlier and a faster depletion (Fig. 4.7 and 4.8). The combination of these phenomena led to earlier apparition of stress, increased length of the stress period, and increased stress intensity. The stress simulated could have dramatic effects on plant growth at BAR. In fact, the average intensity more than doubled and the absence of stress became exceptional. On the contrary, at TOM, the consequences of water stress could be limited. In fact, even applying the weather conditions of BAR did not raise the stress up to the levels at this site, and the absence of stress remained frequent. Again, this probably reflects the differences in soil properties between BAR and TOM. Despite its lower W_{FC} (153 mm on the first 120 cm of soil in forest) than BAR (181 mm), TOM may have a higher water retention capacity, possibly in relation to a higher clay content, notably in the deep layers.

A thorough discussion of the specific impacts of the snow variations, in particular concerning the period of the snow-melt and the drainage, is proposed in a section below.

4.4.2 Role of the snow cover

The difference in winter soil temperature between BAR and TOM—the soil was colder while the air temperature was warmer at BAR than at TOM (e.g. Fig. 4.1 vs Fig. 4.3)—suggests that the height of the snow cover influenced the soil thermal

regime, acting as an insulation material protecting, or even completely preventing, the soil from freezing. In fact, the average snow level was lower at BAR than at TOM. The snow manipulation confirmed this since the increase in snow height reduced (winter 2013–2014) and prevented (winter 2014–2015) soil frost at BAR forest and grassland (Fig. 4.1 and 4.2). At TOM, the normal snow levels were sufficient to prevent soil freezing, explaining the absence of snow manipulation effects until the snow-melt. Such an effect of increased snow height on soil temperature was observed in many snow manipulation experiments (e.g. Brooks et al. 1998; Nobrega and Grogan 2007; Schimel et al. 2004). The snow height threshold at which the snow-pack loose its capacity to decouple air and soil temperature was not determined in this study. However, we were probably working around this threshold at BAR. At the period of melting, a thicker snow-pack delayed the date where the soil temperature started to increase, as shown by the snow manipulations in both BAR and TOM (up to 10 days at BAR forest). This was often observed under increased snow treatments in the field (e.g. Brooks et al. 1998; Nobrega and Grogan 2007; Schimel et al. 2004). However, it has been suggested that, due to the concurrent air warming trend, a deeper snow-pack is likely to melt faster, and therefore snow-melt may not be considerably delayed (Wipf and Rixen 2010). Finally, the thermal state of the soil, that is to say frozen or not, at the establishment of a seasonally permanent snow-pack appeared to be of importance for the rest of the winter (Groffman et al. 2001; Iwata et al. 2010; Olsson et al. 2003). In fact, when the snow-pack develops on a frozen soil, it seems an increase in the snow height do not permit the soil to warm up to 0 °C, as observed at BAR in the winter 2013–2014.

Concerning the soil water content, the snow manipulation did not yield any clear effect of an increased snow cover. This might be related to the relatively high spatial variability reported by the soil moisture sensors (adding thus considerable "noise" around the signal). At TOM, the soil being already saturated with water at snow-melt and runoff occurring at this moment over the soil surface, it is probable that such a snow manipulation cannot modify the water input into the soil. In addition, it is possible that the manipulation of the snow (particularly using the snow blower) modified the physical properties of the snow-pack, notably the snow water equivalent (amount of water contained per unit of snow, e.g. volume or mass). Nevertheless, the results suggest that the peak of soil moisture at snow-melt could be delayed by a few days and be higher under an increased snow height, notably at BAR forest (Fig. 4.1).

The water budget simulations provided more informations on the importance of snow cover and the potential impacts of its variations on soil water dynamics. First, snow constitutes the main pool of water recharging the soil water reserve (Fig. 4.7 and 4.8). In a site like BAR, the variation in the amount of snow (thus the amount of water issued at melting), together with the intensity of the soil water content depletion in the previous vegetation season, directly impacts the level of the soil

water reserve refilling. Particularly under modified climatic conditions, only the run 3—i.e. drier climatic conditions except in winter where the snow is increased in comparison with the current levels—permitted to set-back the REW to 1 at snow-melt (Fig. 4.7). On the contrary, at TOM, even snow conditions similar to those of BAR permit a complete refilling of the water reserve at snow-melt under modified climatic conditions (Fig. 4.8). As a consequence, the number of stress days and the annual stress intensity would directly be related to the amount of snow at BAR but not at TOM since the beginning of the stress depends on the level of REW at the beginning of the vegetation season. Finally, it is when snow melts that most of the drainage occurs and, for both the sites studied, variations in the snow quantity may greatly impact the drainage. The levels of drainage can only be understood in function of the level of REW at the end of the preceding vegetation season. In fact, a snow increase under overall drier climatic conditions (run 2 vs run 1) did not automatically raise the drainage at the level of the control (Fig. 4.7 and 4.8). This is because of the partitioning of water between the refilling of the soil water capacity and the drainage: the lower the water content at the snow-melt is, the higher proportion of water stored is and the lower the drainage is. As a consequence, the simulations performed suggest that under drier climatic conditions in the vegetation season, only an increase in winter precipitations (i.e. more snow that currently) would induce a greater drainage than today. In addition, the peak of drainage could be translated in time under modified climatic conditions (it was simulated earlier at BAR; Fig. 4.7). However, the water balance model we used does not take into account the thermal state of the soil. In particular, we implicitly made the assumption that the soil was unfrozen during the snow-melt, allowing thus water to circulate as in unfrozen conditions. This assumption may not always be verified at BAR, as suggested by field monitoring (Fig. 4.1 and 4.2). Nevertheless, soil frost strongly affects snow-melt infiltration and runoff, a thick frozen soil layer impeding infiltration and inducing drainage (Iwata et al. 2010). That could be a bias for the drainages simulated at BAR. More precise measurements of the depth of freezing and measurements of drainages are required to verify this.

4.4.3 Consequences for the biogeochemical cycling of nutrients and plant nutrition

We identified several periods in the year which could play a role in the control of plant growth, whether directly, through plant physiology, or indirectly, through impacts on soil biogeochemistry and thus on water and nutrient availability for plants. In the light of the results reported in the literature, we initiate a brief discussion on the potential impacts of the soil temperature and water dynamics on both plant physiology and biogeochemical processes at these periods. The questions which

could be addressed here are: (i) When are the conditions of soil temperature and moisture optimum for microbial and enzymatic activities? (ii) Do these periods fit with the period of plant requirement for nutrients? (iii) How can climate related events (e.g. soil frost, snow-melt, summer drought) interfere, positively or negatively, with (i) and (ii) as well as with plant physiology? In other words, what are the "hot-moments" in SW Siberia?

Microbes are responsible for the mineralization of organic matter in the soil and for the release of plant nutrients when they die (cell lysis). Microbial activity requires the presence of liquid water, depends on C substrate availability and is modulated by temperature and moisture (Davidson and Janssens 2006). Microbial substrate and plant nutrient movements in the soil are concomitant with water circulation. Water circulation is controlled by climate, soil properties, vegetation effects and temperature.

Two periods are of importance for the soil moisture content in our driest study site (BAR): the snow-melt, which controls the filling of soil water reserves, and the summer, where these reserves are depleted. These two periods are linked since the same amount of melt-water would not have the same efficiency in refilling the soil water reserve after different levels of depletion, and since the same summer conditions could lead to different levels of depletion depending on the level of refilling at snow-melt. Climate change is expected to modify water dynamics on these periods and vegetation growth might be impacted by new combinations of winter and summer precipitation levels.

In cold ecosystems, soil freezing has a great influence on biogeochemical processes. A frozen soil impedes water circulation and so substrate and nutrient flows in the soil matrix (Davidson and Janssens 2006). But in the same time, the water expansion induced by freezing can induce the lysis of microbial cells (Larsen et al. 2002; Skogland et al. 1988; Yanai et al. 2004), the disruption of soil aggregates (Oztas and Fayetorbay 2003; Six et al. 2004) and the break-up of plant material (Harris and Safford 1996; Melick and Seppelt 1992). In subsequent thawing events, particulate and soluble material released during freezing events are susceptible to constitute inputs for microbial activity and plant nutrition (Jusselme et al. 2016). However, they can also be exported from the system, and possibly lost for microbial activity and/or plant nutrition (DeLuca et al. 1992; Fitzhugh et al. 2001; Vaz et al. 1994; Wang and Bettany 1993). Soil freezing also affects soil micro-fauna (Dörsch et al. 2004; Sjursen et al. 2005; Sulkava and Huhta 2003) and reduces soil compaction (Unger 1991). It affects plant physiology, notably in early winter or lasting over winter, through the damage of roots or root-symbionts and can increase tree mortality (Cleavitt et al. 2008; Kreyling et al. 2012; Repo et al. 2014; Tierney et al. 2001), depending on the hydrological conditions.

Contrasting results have been reported about the overall impact of increased freeze–thaw cycles number, frequency and intensity as well as an important spatial

variability (Henry 2007). However, changes in the composition of soil microbial community (Larsen et al. 2002; Lipson and Schmidt 2004; Sharma et al. 2006; Walker et al. 2006) and in the dynamics of microbes, carbon (labile, dissolved organic C, inorganic C) and nutrients (particularly N) (Brooks et al. 1998; DeLuca et al. 1992; Grogan et al. 2004; Haei and Laudon 2015; Lipson et al. 2000; Schadt 2003; Schimel and Clein 1996; Shibata et al. 2013; Six et al. 2004; Sjursen et al. 2005) were often observed as a result of a modified freeze–thaw cycles regime. In SW Siberia, such freeze–thaw cycle events might be exacerbated at the beginning and at the end of winter, when there is no snow-pack or when it is too shallow to protect soil from freezing. Severe decreases in snow-cover and/or alternation of shorter snow periods seems to be necessary to allow such events occurring during winter, if this could occur episodically as an extreme event at BAR, it seems to be an unlikely possibility at TOM. In fact, climate projections rather indicate an increase in snow height in SW Siberia (Bulygina et al. 2011, 2010, 2009; Cohen et al. 2012; Groisman et al. 2006; Shkolnik et al. 2010).

Warmer soil temperature allowed by higher snow height might stimulate microbial activity over winter. Enhanced respiration (carbon fluxes) and nitrogen cycling activities were reported under experimentally increased snow cover (Nobrega and Grogan 2007; Schimel et al. 2004; Walker et al. 1999). Increased N retention and lower exports were also observed under deeper snow-packs (Brooks et al. 1998; Lewis and Grant 1980; Mitchell et al. 1996; Peters and Leavesley 1995), probably due to a higher microbial N immobilization (Brooks and Williams 1999; Buckeridge and Grogan 2010). However, there is a threshold above which the increase of snow height might not impact anymore soil temperature. It is possible that such a threshold is already reached in situations like TOM.

At snow-melt, soil temperature is buffered by melting snow, soil moisture is high, and the potential for transport to surface water is the greatest. At our study sites, almost all the yearly drainage occurs at snow-melt and climate is likely to impact the amount (our simulations induced variations up to a factor 3) and the timing of drainage. In Arctic ecosystems, it has been proposed that the size of the microbial biomass and soil solution nutrient pool at the end of winter may control the quantity of nutrients available to plants in the following spring (Buckeridge and Grogan 2008). While the micro-organisms remain active over winter under deep snow-packs, they might become increasingly C-limited and would not support the rapid change in soil temperature and moisture at snow-melt (Buckeridge and Grogan 2008; Lipson et al. 2000; Schmidt and Lipson 2004). Their lysis at snow-melt would induce a spring flush of nutrients (Buckeridge and Grogan 2008).

Whether the nutrients are lost for plants may depends on the intensity of runoff and leaching, and on the capacity of the soil to store elements (e.g. by adsorption on particles and/or by immobilization into the microbial biomass) in available forms in the horizons explored by fine roots. Finally, the synchrony with the beginning of

plant activity would be or great importance on their capacity to capture nutrients when they are possibly released in great quantities. In a site like TOM, the relatively deep snow-pack could be beneficial for microbial activity at wintertime but the water-saturation of the soil at snow-melt induce relatively high levels of drainage and/or runoff. In addition, relatively shallow root systems (Chap. 5, Brédoire et al. 2016b) would not permit to absorb the nutrients pushed down into deep soil layers by piston flow. At BAR, soil temperature is often below 0 °C in winter, potentially limiting microbial activity, the drainage is relatively low and root systems are deeper. In such a situation, we can imagine limited nutrient losses for plants at snow-melt. However, it is likely that drainage levels, and possibly winter soil temperature, will be modified with climate change. Multiple possibilities were highlighted by our simulations of the water budget, they would have different impacts on nutrient availability.

4.5 Conclusion

Our two study sites present a similar general pattern in yearly soil temperature and moisture dynamics: temperature is buffered around 0 °C in winter and peaks at its maximum in the middle of summer, the soil water reserve is filled at spring and depleted in summer. However, the joined effects of climate, soil properties and vegetation modulate these dynamics. Overall, BAR experiences drier conditions than TOM and its soil water budget is highly dependent on both intensities of refilling and depletion of water.

Winter, and in particular the snow-cover, exerts a major influence on the dynamics of soil temperature and moisture. The snow-pack buffers soil temperature and eventually prevents freezing. Soil freezing depends notably on the thickness of the snow-pack but also on the status of the soil at the settling of the seasonal snow cover. Typically, soil does not freeze at wintertime at TOM because of a deep snow-cover while it usually freezes at BAR where the snow cover is shallower and appears later, when the soil can already be frozen. Depending on the level of the soil water reserve at the end of autumn, snow-melt has a great importance for recharging this reserve—typically at BAR where the soil is not recharged at autumn—or is associated with drainage—typically at TOM where autumn precipitations often recharge the soil.

Our simulations suggest an increase of water limitations in both forest-steppe and sub-taiga with climate change. This phenomenon would be driven by warmer temperatures and earlier vegetation seasons and be modulated by the amounts of winter precipitations, i.e. snow. In the south, long and intense water shortages are likely to become the usual situation. In the north, they may appear and occur at higher frequency but, even under the current southern climatic conditions, water

stress might be modulated by soil properties. In both cases, an earlier vegetation season would increase the water depletion of the soil profile, and induce earlier apparition, longer duration, and higher intensity of water-stress.

To conclude, snow appears as a "hot-variable" controlling both soil temperature and moisture regimes in SW Siberia. Winter related processes may contribute for a great proportion in the control of biogeochemical processes, and thus of vegetation activity and productivity in this region. The modification of climate, and in particular winter snowfall, is likely to impact those soil temperature and moisture regimes. However, additional measurements (e.g. drainage, soil solution elemental composition, microbial activity, N processes) are required in our study sites to approach mechanisms and infer on their evolution with global change. They will also help determining the "hot-moments" for nutrient availability or loss from the soil–plant system.

Acknowledgements

S. Didier and J. Ranger trained F. Brédoire, in France, for the setting of soil moisture sensors in the field.

References

Arndt, D. S., Baringer, M. O., and Johnson, M. R. (2010). State of the Climate in 2009. *Bulletin of the American Meteorological Society* 91.7, s1–s222. DOI: 10.1175/bams-91-7-stateoftheclimate.

Bassirirad, H. (2000). Kinetics of nutrient uptake by roots: responses to global change. *New Phytologist* 147.1, 155–169. DOI: 10.1046/j.1469-8137.2000.00682.x.

Brooks, P. D. and Williams, M. W. (1999). Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrological Processes* 13.14–15, 2177–2190. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2177::AID-HYP850>3.0.CO;2-V.

Brooks, P., Williams, M., and Schmidt, S. (1998). Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry* 43 (1), 1–15. DOI: 10.1023/A:1005947511910.

Buckeridge, K. M. and Grogan, P. (2008). Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. *Applied Soil Ecology* 39.2, 210–222. DOI: 10.1016/j.apsoil.2007.12.010.

Buckeridge, K. M. and Grogan, P. (2010). Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. *Biogeochemistry* 101.1-3, 105–121. DOI: 10.1007/s10533-010-9426-5.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Korshunova, N. N. (2011). Changes in snow cover characteristics over Northern Eurasia since 1966. *Environmental Research Letters* 6.4, 045204. DOI: 10.1088/1748-9326/6/4/045204.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Radionov, V. F. (2010). Snow cover basal ice layer changes over Northern Eurasia since 1966. *Environmental Research Letters* 5.1, 015004. DOI: 10.1088/1748-9326/5/1/015004.

Bulygina, O. N., Razuvaev, V. N., and Korshunova, N. N. (2009). Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters* 4.4, 045026. DOI: 10.1088/1748-9326/4/4/045026.

Bulygina, O. N., Razuvaev, V. N., Korshunova, N. N., and Groisman, P. Y. (2007). Climate variations and changes in extreme climate events in Russia. *Environmental Research Letters* 2.4, 045020. DOI: 10.1088/1748-9326/2/4/045020.

Cleavitt, N. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Henry, K. S., and Driscoll, C. T. (2008). Effects of soil freezing on fine roots in a northern hardwood forest. *Canadian Journal of Forest Research* 38.1, 82–91. DOI: 10.1139/x07-133.

Cohen, J. L., Furtado, J. C., Barlow, M. A., Alexeev, V. A., and Cherry, J. E. (2012). Arctic warming, increasing snow cover and widespread boreal winter cooling. *Environmental Research Letters* 7.1, 014007. DOI: 10.1088/1748-9326/7/1/014007.

Davidson, E. A. and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440.7081, 165–173. DOI: 10.1038/nature04514.

DeLuca, T. H., Keeney, D. R., and McCarty, G. W. (1992). Effect of freeze-thaw events on mineralization of soil nitrogen. *Biology and Fertility of Soils* 14.2, 116–120. DOI: 10.1007/bf00336260.

Dörsch, P., Palojärvi, A., and Mommertz, S. (2004). Overwinter greenhouse gas fluxes in two contrasting agricultural habitats. *Nutrient Cycling in Agroecosystems* 70.2, 117–133. DOI: 10.1023/b:fres.0000048473.11362.63.

Fitzhugh, R., Driscoll, C., Groffman, P., Tierney, G., Fahey, T., and Hardy, J. (2001). Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. *Biogeochemistry* 56 (2), 215–238. DOI: 10.1023/A:1013076609950.

Giehl, R. F. H. and Wiren, N. von (2014). Root Nutrient Foraging. *Plant Physiology* 166.2, 509–517. DOI: 10.1104/pp.114.245225.

Granier, A., Bréda, N., Biron, P., and Villette, S. (1999). A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* 116.2–3, 269–283. DOI: 10.1016/S0304-3800(98)00205-1.

Groffman, P., Driscoll, C., Fahey, T., Hardy, J., Fitzhugh, R., and Tierney, G. (2001). Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56.2, 135–150. DOI: 10.1023/A:1013039830323.

Grogan, P., Michelsen, A., Ambus, P., and Jonasson, S. (2004). Freeze–thaw regime effects on carbon and nitrogen dynamics in sub-arctic heath tundra mesocosms. *Soil Biology and Biochemistry* 36.4, 641–654. DOI: 10.1016/j.soilbio.2003.12.007.

Groisman, P. Y. and Gutman, G., eds. (2012). *Regional Environmental Changes in Siberia and Their Global Consequences*. Springer Science + Business Media. DOI: 10.1007/978-94-007-4569-8.

Groisman, P. Y., Blyakharchuk, T. A., Chernokulsky, A. V., Arzhanov, M. M., Marchesini, L. B., Bogdanova, E. G., Borzenkova, I. I., Bulygina, O. N., Karpenko, A. A., Karpenko, L. V., Knight, R. W., Khon, V. C., Korovin, G. N., Meshcherskaya, A. V., Mokhov, I. I., Parfenova, E. I., Razuvaev, V. N., Speranskaya, N. A., Tchebakova, N. M., and Vygodskaya, N. N. (2012). Climate changes in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 3, 57–109. DOI: 10.1007/978-94-007-4569-8_3.

Groisman, P. Y., Karl, T. R., Knight, R. W., and Stenchikov, G. L. (1994). Changes of snow cover, temperature, and radiative heat balance over the northern hemisphere. *Journal of Climate* 7.11, 1633–1656. DOI: 10.1175/1520-0442(1994)007<1633:COSCTA>2.0.CO;2.

Groisman, P. Y., Knight, R. W., Razuvaev, V. N., Bulygina, O. N., and Karl, T. R. (2006). State of the ground: Climatology and changes during the past 69 Years over Northern Eurasia for a rarely used measure of snow cover and frozen land. *Journal of Climate* 19.19, 4933–4955. DOI: 10.1175/JCLI3925.1.

Haei, M. and Laudon, H. (2015). Carbon dynamics and changing winter conditions: a review of current understanding and future research directions. *Biogeosciences Discussions* 12.18, 15763–15808. DOI: 10.5194/bgd-12-15763-2015.

Harris, M. M. and Safford, L. O. (1996). Effects of season and four tree species on soluble carbon content in fresh and decomposing litter of temperate forests. *Soil Science* 161.2, 130–135. DOI: 10.1097/00010694-199602000-00008.

Henry, H. A. (2007). Soil freeze–thaw cycle experiments: Trends, methodological weaknesses and suggested improvements. *Soil Biology and Biochemistry* 39.5, 977–986. DOI: 10.1016/j.soilbio.2006.11.017.

IPCC (2013). *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Ed. by T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. Midgley. Cambridge Books Online. Cambridge University Press. 1535 pp. DOI: 10.1017/CBO9781107415324.

Iwata, Y., Hayashi, M., Suzuki, S., Hirota, T., and Hasegawa, S. (2010). Effects of snow cover on soil freezing, water movement, and snowmelt infiltration: A paired plot experiment. *Water Resources Research* 46.9. DOI: 10.1029/2009wr008070.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J. (2012). Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. *Ecology and Evolution* 2.3, 593–614. DOI: 10.1002/ece3.85.

Jusselme, M.-D., Saccone, P., Zinger, L., Faure, M., Roux, X. L., Guillaumaud, N., Bernard, L., Clement, J.-C., and Poly, F. (2016). Variations in snow depth modify N-related soil microbial abundances and functioning during winter in subalpine grassland. *Soil Biology and Biochemistry* 92, 27–37. DOI: 10.1016/j.soilbio.2015.09.013.

Kicklighter, D. W., Cai, Y., Zhuang, Q., Parfenova, E. I., Paltsev, S., Sokolov, A. P., Melillo, J. M., Reilly, J. M., Tchebakova, N. M., and Lu, X. (2014). Potential influence of climate-induced vegetation shifts on future land use and associated land carbon fluxes in Northern Eurasia. *Environmental Research Letters* 9.3, 035004. DOI: 10.1088/1748-9326/9/3/035004.

Kreuzwieser, J. and Gessler, A. (2010). Global climate change and tree nutrition: influence of water availability. *Tree Physiology* 30.9, 1221–1234. DOI: 10.1093/treephys/tpq055.

Kreyling, J., Peršoh, D., Werner, S., Benzenberg, M., and Wöllecke, J. (2012). Short-term impacts of soil freeze-thaw cycles on roots and root-associated fungi of Holcus lanatus and Calluna vulgaris. *Plant and Soil* 353 (1-2), 19–31. DOI: 10.1007/s11104-011-0970-0.

Larsen, K. S., Jonasson, S., and Michelsen, A. (2002). Repeated freeze–thaw cycles and their effects on biological processes in two arctic ecosystem types. *Applied Soil Ecology* 21.3, 187–195. DOI: 10.1016/s0929-1393(02)00093-8.

Legout, A., K., H., Heijden, G. V. der, J-P., L., L., A., and J., R. (2014). Chemical fertility of forest soils: basic concepts. *Revue Forestière Française* SP, Fr.], ISSN 0035. DOI: 10.4267/2042/56262.

Lewis, W. M. and Grant, M. C. (1980). Relationships between Snow Cover and Winter Losses of Dissolved Substances from a Mountain Watershed. *Arctic and Alpine Research* 12.1, 11. DOI: 10.2307/1550586.

Lipson, D. A. and Schmidt, S. K. (2004). Seasonal Changes in an Alpine Soil Bacterial Community in the Colorado Rocky Mountains. *Applied and Environmental Microbiology* 70.5, 2867–2879. DOI: 10.1128/aem.70.5.2867-2879.2004.

Lipson, D. A., Schmidt, S. K., and Monson, R. K. (2000). Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. *Soil Biology and Biochemistry* 32.4, 441–448. DOI: 10.1016/s0038-0717(99)00068-1.

Lucht, W., Schaphoff, S., Erbrecht, T., Heyder, U., and Cramer, W. (2006). Terrestrial vegetation redistribution and carbon balance under climate change. *Carbon Balance and Management* 1.1, 6. DOI: 10.1186/1750-0680-1-6.

Melick, D. R. and Seppelt, R. D. (1992). Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. *Antarctic Science* 4.04, 399–404. DOI: 10.1017/s0954102092000592.

Mitchell, M. J., Driscoll, C. T., Kahl, J. S., Murdoch, P. S., and Pardo, L. H. (1996). Climatic Control of Nitrate Loss from Forested Watersheds in the Northeast United States. *Environmental Science and Technology* 30.8, 2609–2612. DOI: 10.1021/es9600237.

Monteith, J. L. and Unsworth, M. H. (2013). Steady-state heat balance. In: *Principles of Environmental Physics*, 217–247. DOI: 10.1016/b978-0-12-386910-4.00013-5.

Nobrega, S. and Grogan, P. (2007). Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in birch hummock tundra. *Ecosystems* 10 (3), 419–431. DOI: 10.1007/s10021-007-9033-z.

Olsson, P. Q., Sturm, M., Racine, C. H., Romanovsky, V., and Liston, G. E. (2003). Five Stages of the Alaskan Arctic Cold Season with Ecosystem Implications. *Arctic, Antarctic, and Alpine Research* 35.1, 74–81. DOI: 10.1657/1523-0430(2003)035[0074:fsotaa]2.0.co;2.

Oztas, T. and Fayetorbay, F. (2003). Effect of freezing and thawing processes on soil aggregate stability. *Catena* 52.1, 1–8. DOI: 10.1016/s0341-8162(02)00177-7.

Peters, N. E. and Leavesley, G. H. (1995). Biotic and abiotic processes controlling water chemistry during snowmelt at rabbit ears pass, Rocky Mountains, Colorado, U.S.A. *Water, Air, and Soil Pollution* 79.1-4, 171–190. DOI: 10.1007/bf01100436.

Ranger, J. and Turpault, M.-P. (1999). Input–output nutrient budgets as a diagnostic tool for sustainable forest management. *Forest Ecology and Management* (122), 139–154.

Rawlins, M. A., Steele, M., Holland, M. M., Adam, J. C., Cherry, J. E., Francis, J. A., Groisman, P. Y., Hinzman, L. D., Huntington, T. G., Kane, D. L., Kimball, J. S., Kwok, R., Lammers, R. B., Lee, C. M., Lettenmaier, D. P., McDonald, K. C., Podest, E., Pundsack, J. W., Rudels, B., Serreze, M. C., Shiklomanov, A., Skagseth, Ø., Troy, T. J., Vörösmarty, C. J., Wensnahan, M., Wood, E. F., Woodgate, R., Yang, D., Zhang, K., and Zhang, T. (2010). Analysis of the Arctic System for Freshwater Cycle Intensification: Observations and Expectations. *Journal of Climate* 23.21, 5715–5737. DOI: 10.1175/2010jcli3421.1.

Rennenberg, H., Dannenmann, M., Gessler, A., Kreuzwieser, J., Simon, J., and Papen, H. (2009). Nitrogen balance in forest soils: nutritional limitation of plants under climate change stresses. *Plant Biology* 11, 4–23. DOI: 10.1111/j.1438-8677.2009.00241.x.

Repo, T., Sirkiä, S., Heinonen, J., Lavigné, A., Roitto, M., Koljonen, E., Sutinen, S., and Finér, L. (2014). Effects of frozen soil on growth and longevity of fine roots of Norway spruce. *Forest Ecology and Management* 313, 112–122. DOI: 10.1016/j.foreco.2013.11.002.

Robinson, D. A., Dewey, K. F., and Heim, R. R. (1993). Global Snow Cover Monitoring: An Update. *Bulletin of the American Meteorological Society* 74.9, 1689–1696. DOI: 10.1175/1520-0477(1993)074<1689:gscmau>2.0.co;2.

Sadras, V. and Milroy, S. (1996). Soil-water thresholds for the responses of leaf expansion and gas exchange: A review. *Field Crops Research* 47.2-3, 253–266. DOI: 10.1016/0378-4290(96)00014-7.

Schadt, C. W. (2003). Seasonal Dynamics of Previously Unknown Fungal Lineages in Tundra Soils. *Science* 301.5638, 1359–1361. DOI: 10.1126/science.1086940.

Schaphoff, S., Reyer, C. P., Schepaschenko, D., Gerten, D., and Shvidenko, A. (2016). Tamm Review: Observed and projected climate change impacts on Russia's forests and its carbon balance. *Forest Ecology and Management* 361, 432–444. DOI: 10.1016/j.foreco.2015.11.043.

Schimel, J. P., Bilbrough, C., and Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry* 36.2, 217–227. DOI: 10.1016/j.soilbio.2003.09.008.

Schimel, J. P. and Clein, J. S. (1996). Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biology and Biochemistry* 28.8, 1061–1066. DOI: 10.1016/0038-0717(96)00083-1.

Schmidt, S. and Lipson, D. (2004). Microbial growth under the snow: Implications for nutrient and allelochemical availability in temperate soils. *Plant and Soil* 259.1/2, 1–7. DOI: 10.1023/b:plso.0000020933.32473.7e.

Schoenholtz, S., Miegroet, H., and Burger, J. (2000). A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. *Forest Ecology and Management* 138.1-3, 335–356. DOI: 10.1016/s0378-1127(00)00423-0.

Sharma, S., Szele, Z., Schilling, R., Munch, J. C., and Schloter, M. (2006). Influence of Freeze–Thaw Stress on the Structure and Function of Microbial Communities and Denitrifying Populations in Soil. *Applied and Environmental Microbiology* 72.3, 2148–2154. DOI: 10.1128/aem.72.3.2148-2154.2006.

Shibata, H., Hasegawa, Y., Watanabe, T., and Fukuzawa, K. (2013). Impact of snowpack decrease on net nitrogen mineralization and nitrification in forest soil of northern Japan. *Biogeochemistry* 116.1-3, 69–82. DOI: 10.1007/s10533-013-9882-9.

Shkolnik, I. M., Nadyozhina, E. D., Pavlova, T. V., Molkentin, E. K., and Semioshina, A. A. (2010). Snow cover and permafrost evolution in Siberia as simulated by the MGO regional climate model in the 20th and 21st centuries. *Environmental Research Letters* 5.1, 015005. DOI: 10.1088/1748-9326/5/1/01500510.1088/1748-9326/5/1/015005.

Shuman, J. K., Tchebakova, N. M., Parfenova, E. I., Soja, A. J., Shugart, H. H., Ershov, D., and Holcomb, K. (2015). Forest forecasting with vegetation models across Russia. *Canadian Journal of Forest Research* 45.2, 175–184. DOI: 10.1139/cjfr-2014-0138.

Six, J., Bossuyt, H., Degryze, S., and Denef, K. (2004). A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research* 79.1, 7–31. DOI: 10.1016/j.still.2004.03.008.

Sjursen, H., Michelsen, A., and Holmstrup, M. (2005). Effects of freeze–thaw cycles on microarthropods and nutrient availability in a sub-Arctic soil. *Applied Soil Ecology* 28.1, 79–93. DOI: 10.1016/j.apsoil.2004.06.003.

Skogland, T., Lomeland, S., and Goksøyr, J. (1988). Respiratory burst after freezing and thawing of soil: Experiments with soil bacteria. *Soil Biology and Biochemistry* 20.6, 851–856. DOI: 10.1016/0038-0717(88)90092-2.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S., and Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56.3–4, 274–296. DOI: 10.1016/j.gloplacha.2006.07.028.

Sulkava, P. and Huhta, V. (2003). Effects of hard frost and freeze-thaw cycles on decomposer communities and N mineralisation in boreal forest soil. *Applied Soil Ecology* 22.3, 225–239. DOI: 10.1016/s0929-1393(02)00155-5.

Takala, M., Pulliainen, J., Metsamaki, S., and Koskinen, J. (2009). Detection of Snowmelt Using Spaceborne Microwave Radiometer Data in Eurasia From 1979 to 2007. *IEEE Trans. Geosci. Remote Sensing* 47.9, 2996–3007. DOI: 10.1109/tgrs.2009.2018442.

Tchebakova, N. M., Parfenova, E. I., Lysanova, G. I., and Soja, A. J. (2011). Agroclimatic potential across central Siberia in an altered twenty-first century. *Environmental Research Letters* 6.4, 045207. DOI: 10.1088/1748-9326/6/4/045207.

Tchebakova, N. M., Parfenova, E., and Soja, A. J. (2009). The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4.4, 045013. DOI: 10.1088/1748-9326/4/4/045013.

Tchebakova, N. M., Rehfeldt, G. E., and Parfenova, E. I. (2010). From vegetation zones to climatypes: Effects of climate warming on Siberian ecosystems. In: *Permafrost Ecosystems. Siberian Larch Forests*. Chap. 22, 427–447.

Tierney, G., Fahey, T., Groffman, P., Hardy, J., Fitzhugh, R., and Driscoll, C. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56.2, 175–190. DOI: 10.1023/A:1013072519889.

Tóth, B., Weynants, M., Nemes, A., Makó, A., Bilas, G., and Tóth, G. (2015). New generation of hydraulic pedotransfer functions for Europe. *European Journal of Soil Science* 66.1, 226–238. DOI: 10.1111/ejss.12192.

Unger, P. W. (1991). Overwinter Changes in Physical Properties of No-Tillage Soil. *Soil Science Society of America Journal* 55.3, 778. DOI: 10.2136/sssaj1991.03615995005500030024x.

Vaz, M. D. R., Edwards, A. C., Shand, C. A., and Cresser, M. S. (1994). Changes in the chemistry of soil solution and acetic-acid extractable P following different types of freeze/thaw episodes. *Eur J Soil Science* 45.3, 353–359. DOI: 10.1111/j.1365-2389.1994.tb00519.x.

Walker, M. D., Walker, D. A., Welker, J. M., Arft, A. M., Bardsley, T., Brooks, P. D., Fahnestock, J. T., Jones, M. H., Losleben, M., Parsons, A. N., Seastedt, T. R., and Turner, P. L. (1999). Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes* 13.14–15, 2315–2330. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2315::AID-HYP888>3.0.CO;2-A.

Walker, V. K., Palmer, G. R., and Voordouw, G. (2006). Freeze-Thaw Tolerance and Clues to the Winter Survival of a Soil Community. *Applied and Environmental Microbiology* 72.3, 1784–1792. DOI: 10.1128/aem.72.3.1784-1792.2006.

Wang, F. L. and Bettany, J. R. (1993). Influence of Freeze-Thaw and Flooding on the Loss of Soluble Organic Carbon and Carbon Dioxide from Soil. *Journal of Environment Quality* 22.4, 709. DOI: 10.2134/jeq1993.00472425002200040011x.

Wipf, S. and Rixen, C. (2010). A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research* 29.1, 95–109. DOI: 10.1111/j.1751-8369.2010.00153.x.

Yanai, Y., Toyota, K., and Okazaki, M. (2004). Effects of successive soil freeze–thaw cycles on soil microbial biomass and organic matter decomposition potential of soils. *Soil Science and Plant Nutrition* 50.6, 821–829. DOI: 10.1080/00380768.2004.10408542.

Chapter 5

Distributions of fine root length and mass with soil depth in natural ecosystems of south-western Siberia

Brédoire, F., Nikitich, P., Barsukov, P. A., Derrien, D., Litvinov, A., Rieckh, H., Rusalimova, O., Zeller, B., and Bakker, M. R. (2016). Distributions of fine root length and mass with soil depth in natural ecosystems of southwestern Siberia. *Plant and Soil* 400.1-2, 315–335. DOI: 10.1007/s11104-015-2717-9

Abstract

Aims Forest-steppe and sub-taiga, two main biomes of south-western Siberia, have been predicted to shift and spread northwards with global change. However, ecological projections are still lacking a description of belowground processes in which fine roots play a significant role. We characterized regional fine root patterns in terms of length and mass comparing: (1) sites and (2) vegetation covers.

Methods We assessed fine root length and mass down to one meter in aspen (*Populus tremula*) and in grassland stands on six sites located in the forest-steppe and sub-taiga zones and presenting contrasting climate and soil conditions. We distinguished fine roots over diameter classes and also between aspen and understorey in forest. Vertical fine root exploration, fine root densities and total length and mass were computed for all species. Morphological parameters were computed for aspen.

Results In both forest and grassland, exploration was deeper and total length and mass were higher in forest-steppe than in sub-taiga. Exploration tended to be deeper in forest than in grassland and for trees than for understorey vegetation within forest stands.

Conclusions The differences in rooting strategies are related to both pedoclimatic conditions and vegetation cover. Further investigations on nutrient and water availability and on fine root dynamics should permit a better understanding of these patterns and help predicting their future with global change.

Keywords: fine roots, bioclimatic zones, south-western Siberia, *Populus tremula* L., understorey vegetation, grassland

5.1 Introduction

In the context of global change, understanding the structure and functioning of ecosystems is of primary importance to improve predictions on their future status. Plant growth and productivity are likely to be affected, directly or indirectly, by changes in temperature, precipitation regime and the concentration of atmospheric CO_2. Belowground processes have not been yet well integrated in ecosystem and global scale models. Notably, the description of root processes remains highly simplified in such models (Smithwick et al. 2014; Warren et al. 2015). However, due to the difficulty of accessing roots, factors and mechanisms controlling their dynamics are poorly known.

Roots provide anchorage, storage, transport and uptake of nutrients and water to plants. Within the root system, fine roots (usually defined by a diameter < 2 mm), with or without symbiotic partners (ecto-mycorrhizae, endo-mycorrhizae, bacteria), are responsible for most of nutrient and water acquisition. They play a crucial role in the cycling of carbon (C) and nutrients in forest ecosystems (Berg 1984; Helmisaari et al. 2002; Hendrick and Pregitzer 1993; Joslin and Henderson 1987; Leppälammi-Kujansuu et al. 2014). Some estimates suggest that most of the C present in the mineral soil layers and a large amount of labile C cycling in forest derive from fine roots (Kalyn and Rees 2006; Richter et al. 1999). They also represent about one third of global annual net primary productivity (Jackson et al. 1997). Fine roots represent a lower proportion than coarse roots in root biomass stock assessments. For example, in boreal forests they represent about 16 % of the total root biomass (Yuan and Chen 2010). However, their turnover is quicker and their decomposability easier so they contribute substantially more to root production—73 % in boreal forest—and to annual C fluxes through the root system (Pregitzer et al. 2002; Ruess et al. 2003; Yuan and Chen 2010).

In forests, roots originate both from trees and understorey vegetation. The latter, either woody or herbaceous, usually represents a marginal proportion of the aboveground and total biomass (Moore et al. 2007; Shepashenko et al. 1998) but may represent a far larger proportion belowground (Achat et al. 2008; Bakker et al. 2006; Gonzalez et al. 2013; Hansson et al. 2013; Helmisaari et al. 2007). Thus, the understorey vegetation may play a significant role in nutrient fluxes on the ecosystem scale (Moore et al. 2007; Whigham 2004; Yarie 1980). Depending on species and site specificities, competition for resources (e.g. light, water, nutrients) or mutual facilitation (e.g. redistribution of nutrients and/or water, enhancing of litter quality, symbiotic N fixation) could occur (Schenk 2006). It is therefore of interest to specifically distinguish between both trees and understorey roots; this has often been ignored in the literature (Finér et al. 2011a). Furthermore, there is increasing evidence that functional subdivisions occur within fine roots: branching forms, orders and diameter classes differ in term of morphology, physiology, life

history, activity and responses to environmental factors (Guo et al. 2008; Iversen 2014; Keel et al. 2012; King et al. 2002; Kong et al. 2014; McCormack et al. 2015; Pregitzer et al. 1998; Pregitzer 2002; Pregitzer et al. 2002, 1997; Smith et al. 2014; Valenzuela-Estrada et al. 2008; Wells and Eissenstat 2001).

On the global scale, general fine root patterns, in terms of distribution and quantities (biomass, length) within the soil profile, have been found in relation to terrestrial biome distribution (Jackson et al. 1997). Typically, fine root dynamics (production, turnover, life history) respond to environmental factors such as stand characteristics (e.g. species, age, density), soil properties (e.g. nutrient stocks, pH) and climatic features (Finér et al. 2011b; Gill and Jackson 2000; Hendricks et al. 2006; Joslin et al. 2000; Leuschner and Hertel 2003; McCormack et al. 2014, 2013; McCormack and Guo 2014; Yuan and Chen 2010, 2012a,b). Results are not always convergent on how root parameters respond to given environmental factors. Besides this, fine root dynamics vary on the time scale, seasonally and from year to year (Steinaker et al. 2010; Vogt et al. 1998).

Siberia covers several bioclimatic zones, from south to north: steppe, forest-steppe, sub-taiga, southern taiga, middle taiga, northern taiga, forest tundra and tundra. Due to climate change, the locations of these biomes have been predicted to shift northwards and their relative size to change (Jiang et al. 2012; Soja et al. 2007; Tchebakova et al. 2009, 2010). Notably, the space occupied by steppe and forest-steppe may increase at the expense of taiga. Hydrological and fire regimes may be reshaped on the whole territory (Shiklomanov and Lammers 2009; Shkolnik et al. 2010; Soja et al. 2007). As an original feature of climate change in western Siberia, the spatial distribution of the snow cover has been modified and regional increases of snow mass accumulation during winter have occurred and are predicted for this century (Bulygina et al. 2011, 2010, 2009; Groisman et al. 2006; Shkolnik et al. 2010). Ecological processes are likely to be affected by these changes leading to new potentials for land occupation (Bergen et al. 2012). In particular, the southern parts of Western and Central Siberia may become climatically more suitable for many crops (Tchebakova et al. 2011), creating thus a hotspot for food production for the population of central Asia and China, and possibly attracting populations from surrounding territories (Cabestan et al. 2008; Snegur 2006). South-western Siberia has historically been the most populated area of Siberia due to relatively clement climatic conditions and the occurrence of rich soils such as Chernozems allowing agriculture. Even though there is an increasing interest in Siberian ecosystems, fundamental knowledge is still lacking with regard to processes related to global change, especially belowground processes (Gordov and Vaganov 2010; Groisman and Soja 2009).

This study was set up to identify general fine rooting patterns, important for plant nutrition and thought to be sensitive to climate changes, in south-western Siberia. We addressed the following questions: (1) Are there different fine root

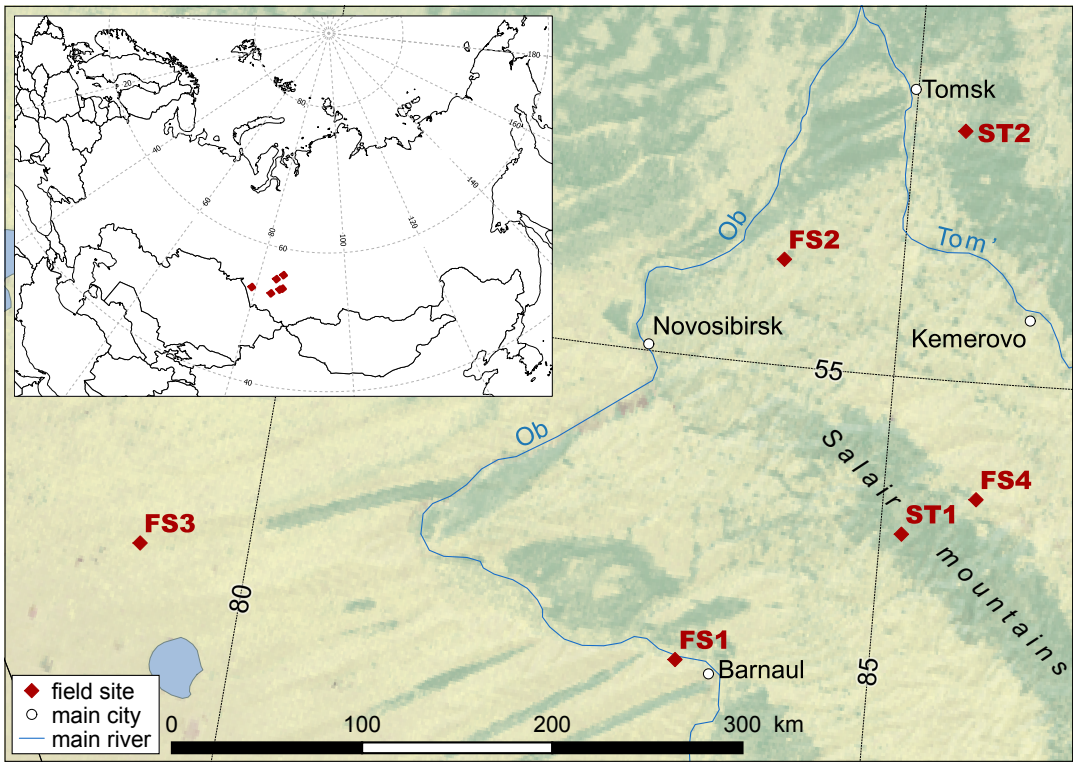


Figure 5.1: Localization of the study sites in Russia (inset) and in south-western Siberia (main map).

patterns, consistent across vegetation covers (here forest and grassland), on the regional scale? In other words, can we distinguish sites or groups of sites? (2) Are there different fine root patterns, consistent across sites, distinguishing vegetation covers? To do this, we sampled fine roots down to 1 m in aspen (*Populus tremula* L.) and in grassland stands located in the transition zone from steppe to sub-taiga and presenting contrasting climate and soil conditions. Based on length and mass measurements, we characterized fine root soil exploration, calculated totals throughout the profile as well as proxies for morphological traits. Finally, we discussed the possible implication of several environmental factors in the control of these fine root patterns and provided hypotheses on their evolution in the context of global change.

Table 5.1: Geographical site characteristics and soil description of the sites studied.

ID	Bioclimatic zone	Name[a]	Lat. N	Long. E	Elev.[b]	Soil in forest[c]	Soil in grassland[c]
FS1	Forest-steppe (Southern part)	Barnaul	53.41	83.47	221	Haplic Phaeozem	Calcic Chernozem
FS2	Forest-steppe (Northern part)	Chebula	55.55	84.00	186	Haplic Phaeozem	Haplic Phaeozem
FS3	Steppe to Forest-steppe	Krasnozerskoye	53.59	79.14	141	Phaeozem	Calcic Hortic Chernozem
FS4	Sub-taiga to Forest-steppe	Salair East	54.39	85.75	305	Leptic Phaeozem	Leptic Phaeozem
ST1	“Blackish taiga”	Salair West	54.18	85.17	358	Haplic Luvisol	
ST2	Sub-taiga	Tomsk	56.30	85.43	232	Albic Luvisol	Albic Luvisol

[a]according to the closest city or geographical area; [b]elevation, in m above sea level; [c]according to WRB (IUSS Working Group WRB 2014)

5.2 Materials and methods

5.2.1 Site description

We selected six sites in south-western Siberia located on the transition from steppe to sub-taiga and with contrasting pedoclimatic conditions (Fig. 5.1 and Table 5.1). Krasnozerskoye (hereafter noted FS3) is located on the border of steppe and forest-steppe, Barnaul (FS1) in the southern part of forest-steppe, Chebula (FS2) in the northern part of forest-steppe, Salair East (FS4) on the transition between sub-taiga and forest-steppe in the foothills of the Salair mountains range, Salair West (ST1) in the "Blackish" taiga belt of Salair mountains, and Tomsk (ST2) in sub-taiga[1]. Sites located in the forest-steppe are expected to be drier, to have higher mean temperatures and to experience a lower height of snow during winter than sites located in the sub-taiga. The same phenomenon is expected from the South to the North, at the exception of ST1 which is located in a low-mountain range and experience climatic conditions close to ST2, our northernmost site.

All soil profiles described in this study have developed on a loess parent material and vegetation cover had comparable features in terms of dominant species composition, stand age and low human impact (i.e. no active management for the last decades; Tables 5.2 and 5.3). Five sites presented almost pure aspen (*Populus tremula* L.; Table 5.2) forest stands and also grassland areas where we made measurements. ST1 only presented forest. All aspen stands had closed canopy. For each site and each vegetation cover, we delimited three study stands spaced by 200–2000 m. Those three stands were considered as replications for each site.

Forest study stands were defined as containing at least 30 *Populus tremula* trees. All trees and shrub species were identified and individual stems counted. We measured the circumference at 1.30 m of all trees, the height of at least 10 trees per replicate using a clinometer (Suunto Optical Reading Clinometer PM-5/400 PC) and estimated diameter and height of all shrubs taller than 1.30 m. On five dominant trees per stand, so 15 per site, we took a tree core with a 5 mm diameter Pressler corer (Suunto) and used it for assessing age by counting of tree rings (Table 5.2). Leaf area index (LAI) was estimated by collecting litterfall in autumn 2013. Five litter traps of 1.96 m^2 each were setup earlier in the season on each site. We sorted the litterfall to keep only the leaves and oven dried them at 60 °C to constant weight. For each site, the surface area and the dry weight of 20 leaves was then used to compute LAI in m^2 leaves m^{-2} ground.

Vegetation cover was described on an area of 100 m^2 in each forest (woody and herbaceous understorey vegetation) and grassland (herbaceous) stand. All species

1. In the corresponding publication, sites were abbreviated differently from the rest of this manuscript. We keep this encoding for the present chapter as its main message is the evidence of distinct fine root patterns between forest-steppe and sub-taiga.

Table 5.2: Forest stand characteristics. Mean and standard error of replicate mean for 3 replicate plots per site.

	Surface	Density (tree ha^{-1})			Basal Area (m^2 ha^{-1})			DBH (cm)		Height (m)		Age (years)		LAI (m^2 m^{-2})	
Site	(m^2)[a]	mean	se	% aspen[b]	mean	se	% aspen[b]	mean	se	mean	se	mean	se	mean	se
FS1	100–325	1664.0	271.9	92.6	34.4	8.7	90.4	14.9	1.1	11.2	0.3	26.9	1.3	4.9	0.6
FS2	800–1050	387.3	39.5	93.2	36.4	3.5	89.9	33.9	0.2	28.0	1.7	61.7	3.4	3.8	0.3
FS3	242–696	767.0	235.4	98.0	42.6	6.8	97.9	26.3	2.3	18.7	1.5	51.0	2.6	3.8	0.3
FS4	156–192	1882.7	145.8	100.0	29.1	1.9	100.0	13.7	0.8	15.7	0.1	21.4	3.8	5.1	0.6
ST1	240–350	1144.0	147.1	95.5	47.5	7.1	97.5	22.8	0.8	24.8	1.1	46.7	1.3	5.0	0.4
ST2	264–420	1139.3	188.8	86.0	43.8	7.6	95.9	21.4	2.6	18.2	2.1	55.8	14.1	2.9	0.5

Only pole and tree stages are included here (i.e. diameter at 1.3 m > 7 cm and height > 1.3 m)

[a]Surface described, plot set to include at least 30 *Populus tremula*

[b]Other tree species: mostly *Betula pendula* but also, very rarely, *Abies sibirica*, *Padus avium*, *Pinus sibirica* and *Pinus sylvestris*

Table 5.3: Composition of the understorey vegetation in forest (herbaceous, shrub and tree species with a height < 1.3 m and a diameter < 1 cm) and herbaceous species in grassland. Range of the number of species over 3 replicates and dominant species.

Site	n[a]	Dominant species[b]
Forest		
FS1	14–18	*Populus tremula* L., *Heracleum sibiricum* L.
FS2	21–27	*Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth
FS4	20–44	*Populus tremula* L., *Carex pallescens* L., *Phlomis tuberosa* L.
ST1	11–17	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth, *Urtica dioica* L.
ST2	16–29	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth
Grassland		
FS1	13–17	*Bromopsis inermis* (Leys.) Holub, *Cuscuta europaea* L., *Festuca pseudovina* Hack. ex Wiesb.
FS2	19–26	*Bromopsis inermis* (Leys.) Holub, *Alopecurus pratensis* L.
FS4	22–60	*Bromopsis inermis* (Leys.) Holub, *Seseli ledebourii* G. Don fil., *Filipendula vulgaris* Moench
ST2	20–21	*Calamagrostis epigeios* (L.) Roth, *Bromopsis inermis* (Leys.) Holub, *Alopecurus pratensis* L.

[a]number of species; [b]we retained species occurring in at least 2 of the 3 site replicates and with a mean score on the Braun-Blanquet scale > 1

were identified and their percent coverage was visually estimated based on the Braun-Blanquet scale (Braun-Blanquet et al. 1932) consisting of a plus sign (sparse and covering a small area) and a series of numbers from 1 to 5 (5 is covering more than 75 % of the area). On each site, we calculated for each species the mean score on the Braun-Blanquet scale (ignoring the "+" class) and assumed species to be dominant when they were present in at least two of the 3 replicates and with a mean score > 1 (Table 5.3).

Climate data for the closest weather station for each site were provided by the Russian Research Institute of Hydrometeorological Information–World Data Centre (RIHMI-WDC) for FS1, FS2, FS3 and ST2, or were collected and merged from National Oceanic and Atmospheric Administration (NOAA) and InfoSPACE for FS4 and ST1. Available data were averaged for the period 1981–2010 (Table 5.4).

5.2.2 Fine root sampling and processing

All samplings were carried out between July 9th and July 25th 2013. On each study stand, we dug a soil pit down to 120 cm, except in FS4 grasslands where we reached a dense schist material around 90 cm. All soil profiles were described according to WRB (IUSS Working Group WRB 2014) (Table 5.1). In each soil pit, bulk soil samples were sampled horizontally with a cylinder of 5.5 cm diameter and 8.0 cm length at the depths of 5, 15, 30, 60 and 100 cm. Litter was sampled over a surface area of 30 by 40 cm close to soil pits. Bulk soil and litter samples were stored at 4 °C until processing in the lab. In order to evaluate whether rooting was much deeper than the vertical surface included in our sampling, we also performed counts on root segments at the bottom of each soil pit. For this we used the biggest undisturbed zone we could delimit (0.15–1.00 m^2) and quantified coarse (> 2 mm in diameter) and fine roots (< 2 mm diameter) separately. At each horizontal surface of inspection we scraped a few cm deep into the undisturbed soil surface to detect and census all the roots present. The intensity of such vertical rooting can be indicative of shallow versus deep soil systems (Achat et al. 2008).

In the lab, all roots were extracted from bulk litter and soil samples using sieves and tweezers. We selected only alive fine roots with a diameter < 2 mm and sorted them by diameter classes: 2–1.2 mm, 1.2–0.8 mm, 0.8–0.4 mm, 0.4–0.2 mm and < 0.2 mm. However, it has been suggested that small sample volume cannot be well representative for the biggest diameter classes of fine roots (Pierret et al. 2005; Taylor et al. 2013). There is also increasing evidence that roots of < 1 mm are the dominant component of the root system (Iversen 2014; Pregitzer 2002). Thus, we present hereafter the results for the diameter classes < 0.8 mm. For forest samples, we also distinguished between aspen and non-aspen (mainly herbaceous understorey vegetation) fine roots based on their visual aspect (colour, size, morphology, branching forms, etc.) and with the help of reference samples taken carefully following aspen

Table 5.4: Climatic features of the study sites. Data averaged on the period 1981–2010. Data presented for each site come from the closest weather stations.

Variable	Period	FS1	FS2	FS3	FS4	ST1	ST2
WMO index of the station		29838	29539	29915	29745	29736	29430
Distance site-station (km)		4	28	76	18	64	38
Air Temperature (°C)	MAT	2.7	1.3	2.9	2.3	1.2	0.9
	DJF	-14.1	-15.2	-15.1	-15.4	-17.6	-15.6
	MAM	3.4	2.0	3.4	3.4	2.8	1.6
	JJA	18.3	17.0	19.7	17.4	16.9	16.7
	SON	2.8	1.2	3.2	3.0	2.2	0.8
Precipitation (mm)	MAP	431.5	509.8	324.5	432.3	453.0	566.5
	DJF	69.8	84.5	53.2	54.3	66.1	104.7
	MAM	85.1	91.3	58.2	78.9	75.1	98.2
	JJA	166.6	184.8	135.3	182.2	168.8	202.9
	SON	107.7	146.4	76.1	106.1	115.9	157.2
Snow Height (cm)	climax*	48.8	42.5	18.8	38.0	54.3	70.6
SCD 1 cm (days)	year	157.2	167.6	141.9	144.5	149.5	178.1
SCD 20 cm (days)	year	108.3	118.3	25.2	88.3	116.4	145.5
Soil Temp. at 20 cm (°C)	DJF	-1.5		-6.0			-0.4
	MAM	4.3		4.0			2.4
	JJA	18.9		20.3			16.4
	SON	6.5		7.3			5.8
Soil frozen at 20 cm (days)	year	86.8		130.1			44.5
Depth of soil frozen (m)	DJF	20–40		40–80			0–20

WMO: World Meteorological Organization; MAT: mean annual temperature;
MAP: mean annual precipitation; SCD: snow cover duration
D, J, F, M, A, M, J, J, A, S, O and N are the months of the year
*climax: maximum snow cover depth, i.e. mean depth between mid-February and mid-March

coarse roots. Total fine root length in the sample was measured according to Tennant (1975). We counted intersects of each set after random disposition of fine roots over a grid of 1 by 1 cm. Fine root length density (FRLD, in $cm\,cm^{-3}$) was calculated according to equation 5.1:

$$\mathrm{FRLD} = \alpha \times \frac{N \times u}{V} \tag{5.1}$$

where $\alpha = 11/14$ (Tennant 1975), N is the number of intersects in the sample, u the grid unit (here 1 cm) and V the volume of the sample (here 190.07 cm^3). After length measurements, we dried roots at 60 °C for 48 h and measured their mass. Fine root mass density (FRMD, in $mg\,cm^{-3}$) was calculated following equation 5.2:

$$\mathrm{FRMD} = \frac{m}{V} \tag{5.2}$$

where m is the mass (mg) of fine roots in the sample. We computed fine root morphological proxies using fine root diameter classes and assuming roots as regular cylinders: specific root length (SRL, in $m\,g^{-1}$) and specific root area (SRA, in $m^2\,kg^{-1}$):

$$\mathrm{SRL} = \frac{1}{10} \times \frac{\mathrm{FRLD}}{\mathrm{FRMD}} \tag{5.3}$$

$$\mathrm{SRA} = \frac{1}{10} \times \sum_{d=0.2}^{0.8} \frac{\pi \times d \times \mathrm{FRLD}_d}{\mathrm{FRMD}_d} \tag{5.4}$$

where d is the maximum diameter of the fine root class (in mm) and FRLD_d and FRMD_d are FRLD and FRMD calculated for the diameter class d, respectively.

5.2.3 Computing of fine root profiles

Five soil layers were defined between 0 and 120 cm according to soil horizon description in each soil pit (horizons were merged or divided in order to have 5 layers corresponding to the 5 sample depths, the profiles studied presented between 4 and 7 horizons, the mean number of horizons of the 33 profiles studied is 5.03). We assumed root densities measured at systematic depths being representative of the mean density for the corresponding soil layers. On this basis, we calculated the total fine root length and the total fine root mass down to 120 cm. Cumulated root profiles were modelled in each soil pit according to Gale and Grigal (1987):

$$Y = 1 - \beta^d \tag{5.5}$$

where Y is the cumulative root proportion (value between 0 and 1) from the soil surface to depth d (cm), and β is the estimated "extinction coefficient". β provides a simple numerical index of the distribution of roots.

Table 5.5: Number of roots going down per m^2 at the bottom of the pit. Results are mean of 3 replicates per site ± standard error. Depth and surface area ranges of observation are given. Different letters denote significant differences at $p < 0.05$ level using a Tukey post-hoc comparison. ANOVA results are given in Table C.1.

		Depth	Surface	Coarse roots (nb m^{-2})			Fine roots (nb m^{-2})		
Veg. cover	Site	(m)	(m^2)	mean	se	stat	mean	se	stat
Forest	FS1	120–120	0.49–0.68	2.0	0.8	ab	19.8	4.3	a
	FS2	112–125	0.35–0.56	1.4	0.3	ab	4.6	0.9	a
	FS3	110–128	0.35–0.51	3.6	0.6	a	17.2	8.4	a
	FS4	118–130	0.25–0.36	0.3	0.2	b	2.2	0.8	a
	ST1	110–120	0.42–0.80	1.3	0.7	ab	8.7	3.3	a
	ST2	115–122	0.15–0.42	0.8	0.5	b	1.9	0.7	a
Grassland	FS1	120–130	0.40–1.00	0.0	0.0	a	20.3	6.0	a
	FS2	120–128	0.35–0.54	0.2	0.2	a	8.9	2.0	a
	FS3	108–115	0.29–0.36	0.0	0.0	a	12.0	2.9	a
	FS4	85–100	0.30–0.48	0.2	0.2	a	12.2	9.6	a
	ST2	107–120	0.30–0.36	0.0	0.0	a	2.5	0.4	a

5.2.4 Statistical analyses and non-linear regression

Comparisons of sites were conducted for each combination of factors (vegetation cover, diameter, species) by Tukey's HSD (Honestly Significant Difference) test following one-way ANOVA with a significance level of $p < 0.05$. ANOVA and non-linear regression assumptions of normality and homogeneity of variance were visually tested with residuals plots and quantile-quantile plots of residuals. All non-linear regressions and statistical analyses were performed with R 3.1.0 (R Core Team 2014).

5.3 Results

5.3.1 Rooting depth

Fine roots were present at the bottom of all the pits from 1.9 to 17.2 roots per m^2 indicating that we did not reach the absolute maximum depth (Table 5.5). No significant difference in the number of fine roots at the bottom of the pit permitted to discriminate between sites. Coarse roots were found at the bottom of the pits in all forest stands and in two grassland stands (FS2 and FS4). In forest, FS3 had the highest number of coarse roots at the bottom of the pit whereas FS4 and ST2 had the lowest (Table 5.5).

5.3.2 Fine roots in the litter layer

The mean fine root length measured in the litter layer ranged from 8.2 to 38.9 m m^{-2} in forest (overall species) and from 0 to 18.7 m m^{-2} in grassland. Respectively, the mean fine root mass ranged from 0.5 to 4.8 g m^{-2} in forest and from 0 to 0.4 g m^{-2} in grassland. Results were highly variable within sites so they did not appear significantly different (Tables C.1 and C.2).

5.3.3 Cumulative fine root length and mass throughout the profile

Significant differences occurred between sites in terms of total fine root length and mass computed down to 120 cm except when considering non-aspen roots in forests. In forest, FS1 exhibited the highest total fine root length and fine root mass whereas ST1 exhibited the lowest values, the values of ST2 were close to ST1 and other sites were in between extremes (Fig. 5.2, Table 5.6). In grassland, FS2 and FS3 exhibited the highest total fine root length and FS4 and ST2 the lowest whereas FS1 and FS3 had the highest total fine root mass and ST2 the lowest (Fig. 5.2, Table 5.6). Total fine root length tended to be higher in grassland (5.21 to 11.71 km m^{-2}) than in forest (1.60 to 6.72 km m^{-2}) whereas total fine root mass was similar (0.20–0.61 and 0.16–0.55 kg m^{-2} in forest and grassland respectively; Table 5.6).

Species composition of total fine root length and mass computed over 120 cm varied between forest sites. More than 50 % of the total fine root length was composed by aspen roots in FS1 and FS3, by non-aspen roots in FS2 and FS4 whereas the proportions were close to 50 % in ST1 and ST2 (Fig. 5.2 and Table C.3). Aspen roots represented a higher biomass than non-aspen roots in all sites except in FS2 (Fig. C.1 and Table C.4).

The biggest diameter classes of fine roots (> 0.8 mm) generally represented less than 5 % of the total fine root length computed over 120 cm (Table C.3). However, they represented 7 to 37 % of the total fine root mass (Table C.4). The smallest diameter class of fine roots (< 0.2 mm) represented the largest part of total fine root length—up to 91 % in grassland (Table C.3)—in accordance with Pregitzer et al. (2002).

5.3.4 Fine root exploration of the soil profile

Fine root length density (FRLD) and fine root mass density (FRMD) were decreasing with soil depth with different rates between sites (Fig. 5.3 and 5.4). In forest, 48.4 to 83.6 % of the total fine root length and 44.2 to 81.2 % of the total fine root mass occurred in the top 30 cm (all species; Table 5.6). FS1 had the lowest proportion of total fine root length and fine root mass in the top 30 cm and ST1 and ST2 the

Table 5.6: Values of the β coefficient from the model of Gale and Grigal (1987) computed on a length basis and on a mass basis, total value of fine root length (FRL) and mass (FRM) down to 120 cm and the percentage of fine root length and mass in the top 30 cm. Mean and standard error of the mean of 3 replicates per site. Different letters denote significant differences at $p < 0.05$ level using a Tukey post-hoc comparison and for a given combination of vegetation cover and species. ANOVA results are given in Table C.1.

		β			Total profile[a]			Top 30 cm (%)			Max[b]
Species	Site	mean	se		mean	se		mean	se		(cm)
Results based on fine root length (FRL)											
Forest											
overall	FS1	0.978	0.003	a	6.72	1.04	a	48.4	4.9	b	206.3
	FS2	0.961	0.007	abc	4.80	1.44	ab	67.8	6.5	ab	117.1
	FS3	0.967	0.005	ab	6.15	1.20	a	62.9	5.6	ab	136.6
	FS4	0.966	0.004	ab	5.97	0.92	ab	64.1	4.3	ab	132.9
	ST1	0.941	0.005	c	1.60	0.02	b	83.6	2.7	a	75.5
	ST2	0.949	0.002	bc	2.47	0.22	ab	79.3	1.2	a	87.5
aspen	FS1	0.979	0.002	a	5.03	0.89	a	47.2	4.0	a	214.6
	FS2	0.961	0.007	a	1.50	0.38	bc	68.0	6.4	a	116.6
	FS3	0.976	0.002	a	3.99	0.93	ac	50.9	3.6	a	192.9
	FS4	0.968	0.010	a	2.15	0.64	abc	58.9	11.2	a	141.9
	ST1	0.945	0.018	a	0.86	0.16	b	76.4	8.9	a	81.9
	ST2	0.958	0.005	a	1.25	0.16	bc	71.7	4.3	a	107.5
non-aspen	FS1	0.970	0.014	a	1.69	1.28	a	55.8	18.1	a	152.7
	FS2	0.959	0.013	a	3.30	1.10	a	67.4	10.8	a	109.0
	FS3	0.930	0.005	a	2.16	0.77	a	88.2	2.0	a	63.9
	FS4	0.948	0.015	a	3.82	0.87	a	74.9	11.1	a	86.5
	ST1	0.872	0.044	a	0.74	0.15	a	93.0	6.0	a	33.6
	ST2	0.932	0.015	a	1.22	0.30	a	85.1	5.3	a	65.8
Grassland											
overall	FS1	0.968	0.003	a	7.86	0.89	ab	62.5	3.0	a	140.1
	FS2	0.963	0.004	a	11.71	1.17	a	67.3	3.6	a	122.3
	FS3	0.967	0.007	a	11.44	0.82	a	62.3	7.0	a	136.4
	FS4	0.954	0.005	a	6.20	0.53	b	75.0	3.4	a	98.1
	ST2	0.930	0.019	a	5.21	0.70	b	84.9	6.1	a	63.5

[a]Total down to 120 cm: FRL is in km m^{-2} and total FRM is in kg m^{-2}; [b]Maximum rooting depth as estimated with the (Gale and Grigal 1987) model and for a cumulated root proportion of 99 %

Table 5.6: Continued

		β			Total profile[a]			Top 30 cm (%)			Max[b]
Species	Site	mean	se		mean	se		mean	se		(cm)
Results based on fine root mass (FRM)											
Forest											
overall	FS1	0.981	0.001	a	0.61	0.10	a	44.2	2.5	b	235.7
	FS2	0.962	0.013	ab	0.33	0.05	ab	64.5	11.7	ab	117.6
	FS3	0.965	0.007	ab	0.39	0.08	ab	63.9	6.7	ab	130.5
	FS4	0.963	0.003	ab	0.51	0.11	ab	67.0	3.2	ab	123.4
	ST1	0.948	0.005	b	0.20	0.01	b	79.4	3.6	a	86.0
	ST2	0.945	0.005	b	0.22	0.04	b	81.2	3.4	a	81.3
aspen	FS1	0.981	0.001	a	0.51	0.15	a	43.1	2.4	b	244.5
	FS2	0.945	0.003	a	0.13	0.03	b	81.6	1.5	a	81.2
	FS3	0.971	0.004	a	0.31	0.07	ab	58.0	4.8	ab	156.9
	FS4	0.967	0.009	a	0.26	0.08	ab	61.2	8.8	ab	137.1
	ST1	0.944	0.016	a	0.13	0.02	b	78.3	7.8	a	80.2
	ST2	0.946	0.010	a	0.14	0.03	b	79.5	5.7	a	82.9
non-aspen	FS1	0.972	0.011	a	0.10	0.07	a	55.4	14.9	a	160.0
	FS2	0.963	0.018	a	0.20	0.02	a	58.9	15.9	a	121.6
	FS3	0.932	0.016	a	0.08	0.02	a	84.8	6.3	a	65.5
	FS4	0.941	0.013	a	0.25	0.09	a	81.6	6.8	a	75.1
	ST1	0.884	0.045	a	0.07	0.03	a	89.8	8.5	a	37.5
	ST2	0.933	0.021	a	0.07	0.02	a	82.8	7.2	a	66.0
Grassland											
overall	FS1	0.962	0.005	a	0.39	0.07	a	68.1	4.8	a	118.8
	FS2	0.955	0.008	a	0.36	0.05	ab	73.3	6.2	a	100.2
	FS3	0.957	0.014	a	0.55	0.03	a	68.3	10.4	a	105.7
	FS4	0.946	0.005	a	0.37	0.03	ab	80.6	3.5	a	82.9
	ST2	0.911	0.033	a	0.16	0.06	b	88.0	5.8	a	49.3

[a]Total down to 120 cm: FRL is in km m^{-2} and total FRM is in kg m^{-2}; [b]Maximum rooting depth as estimated with the (Gale and Grigal 1987) model and for a cumulated root proportion of 99 %

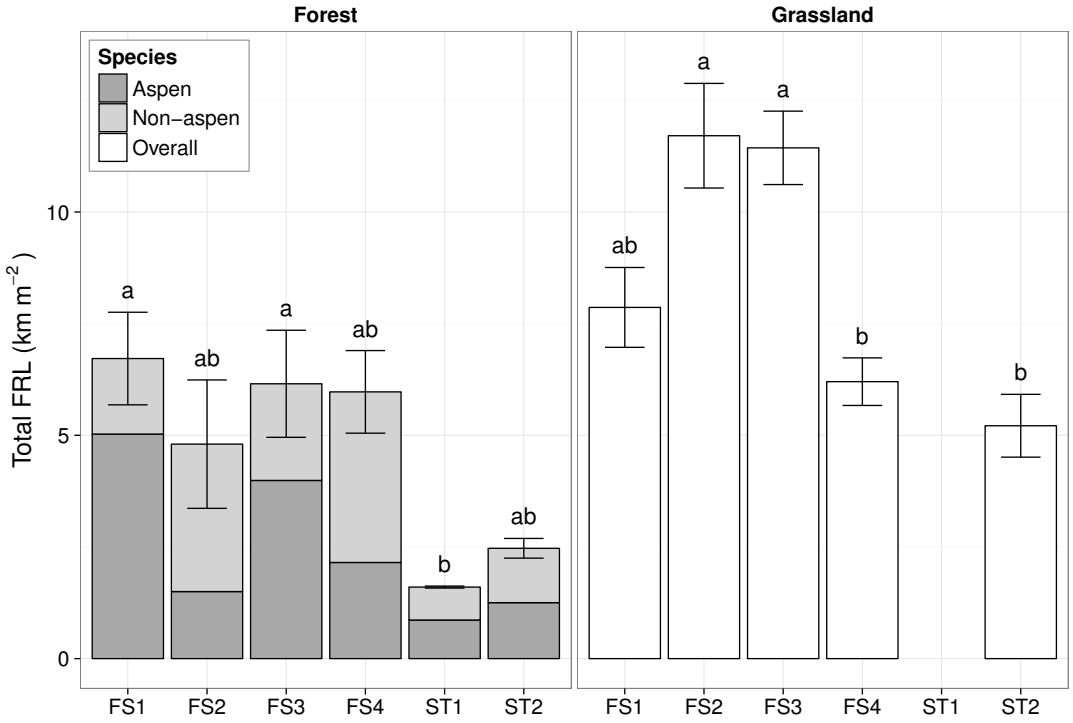


Figure 5.2: Total fine root length over 120 cm in forest (left panel) and grassland (right panel). Mean and standard error of the mean of 3 replicates per site. In forest, total fine root length is detailed for aspen (dark grey) and non-aspen (light grey). Results presented for roots with a diameter < 0.8 mm. Different letters denote significant differences at $p < 0.05$ level using a Tukey post-hoc comparison. ANOVA results are given in Table C.1.

highest. Significant differences between sites were only found for the overall profiles in forests. In grasslands, a similar ranking of sites was possible based on mean values of β but the differences between sites were not significant (Table 5.6).

The β coefficient is a proxy for vertical root distribution. High values of β (e.g. 0.98) are associated with larger proportion of roots at deeper soil depths while low values of β (e.g. 0.92) are associated with larger proportion of roots near the soil surface (Gale and Grigal 1987). At the site level and for each vegetation cover, β values calculated on a length basis were close to calculated on a mass basis (Table 5.6). Differences between sites were only significant in forests when not differentiating for species. FS1 presented the deepest fine root distribution (highest value of β, > 0.96) whereas ST2 and ST1 exhibited the shallowest profile (lowest β, < 0.96), the other sites being in between (Table 5.6, Fig. 5.5 and Fig. C.2). Grassland generally exhibited shallower profiles than forest (Fig. 5.6 and Fig. C.3). In forests, aspen roots generally had deeper profiles than non-aspen ones (Fig. 5.7 and Fig. C.4).

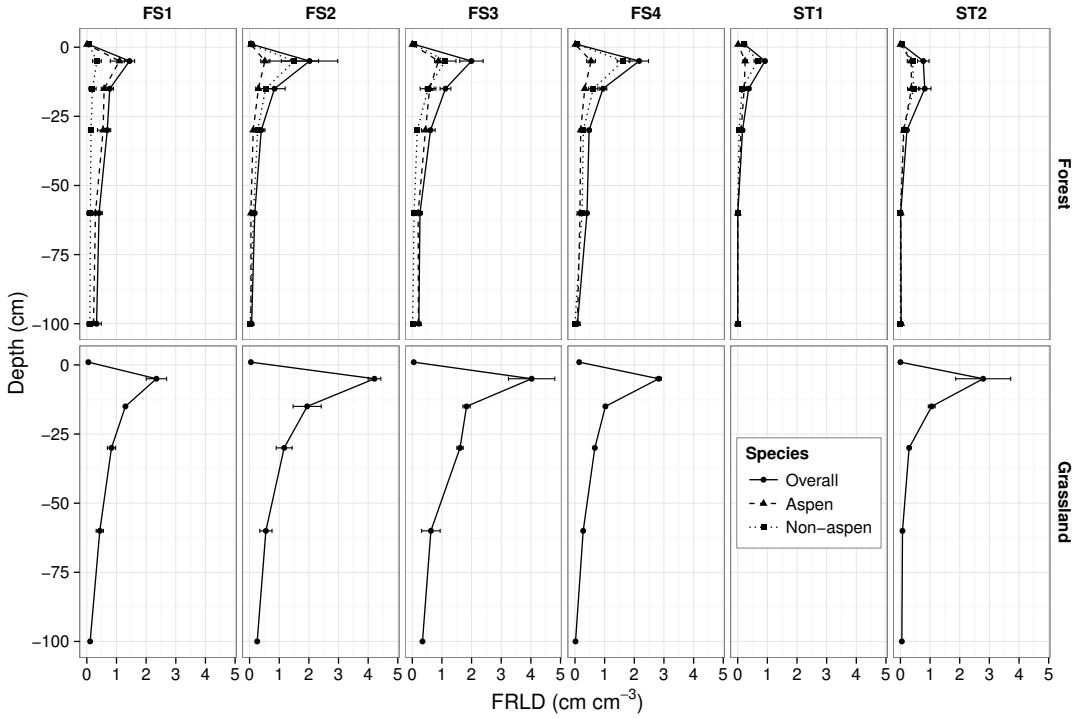


Figure 5.3: Fine root length density (FRLD) profile in forest (upper panels) and grassland (lower panels) litter and soil. Mean and standard error of the mean of 3 replicates per site. Details on species composition are given in forest, non-aspen roots came mainly from understorey vegetation and occasionally from other tree and shrub species. Results presented for roots with a diameter < 0.8 mm.

5.3.5 Aspen fine root morphology

Specific root areas (SRA) and specific root lengths (SRL) of aspen roots were quite similar for the top three soil layers considered (Table 5.7). No significant differences between sites and depths were detected, presumably as a result of a high variability of these values.

5.4 Discussion

In our work we aimed at assessing fine root patterns in forests and grasslands in SW Siberia. This showed differences between grasslands and forests, the latter having deeper rooting patterns. The influence of bioclimatic zones, nutrient and water availability will be discussed.

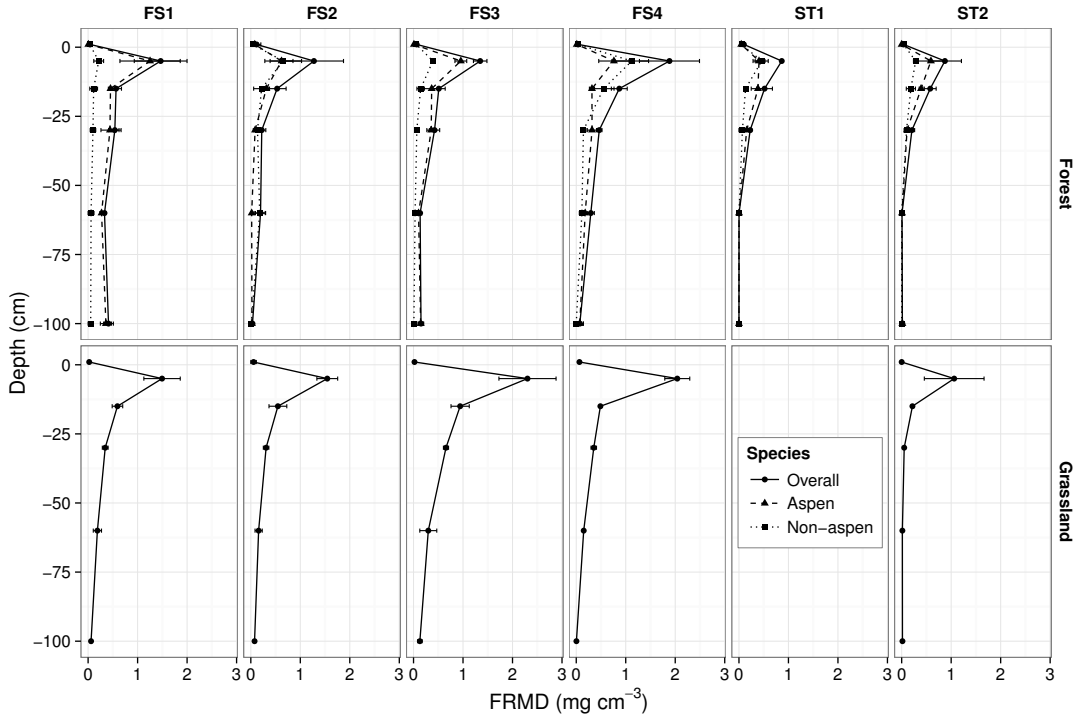


Figure 5.4: Fine root mass density (FRMD) profile in forest (upper panels) and grassland (lower panels) litter and soil. Mean and standard error of the mean of 3 replicates per site. Details on species composition are given in forest, non-aspen roots came mainly from understorey vegetation and occasionally from other tree and shrub species. Results presented for roots with a diameter < 0.8 mm.

5.4.1 Regional fine root patterns

Relation with bioclimatic zones

Our analysis does not allow us to clearly distinguish sites in relation to climatic features. The climate gradient might not be contrasted enough and the variation in other parameters such as soil does not allow disentangling factors. However, two group of sites arose with contrasting fine root patterns. One group includes the sites located in the forest-steppe (FS1 and FS2) and on the limits of this bioclimatic zone (FS3 and FS4). The other group contains the site located in Blackish taiga (ST1) and the one in sub-taiga (ST2). We further refer to these two groups as "forest-steppe" and "sub-taiga". Total fine root length and mass tended to be higher and soil exploration, as reflected by the β coefficient, occurred deeper in forest-steppe than in sub-taiga (Fig. 5.2 and 5.5).

In forests, the β coefficients of our forest-steppe sites (0.961 to 0.981 overall species, Table 5.6) were closer to the mean β of deciduous temperate forest (0.967)

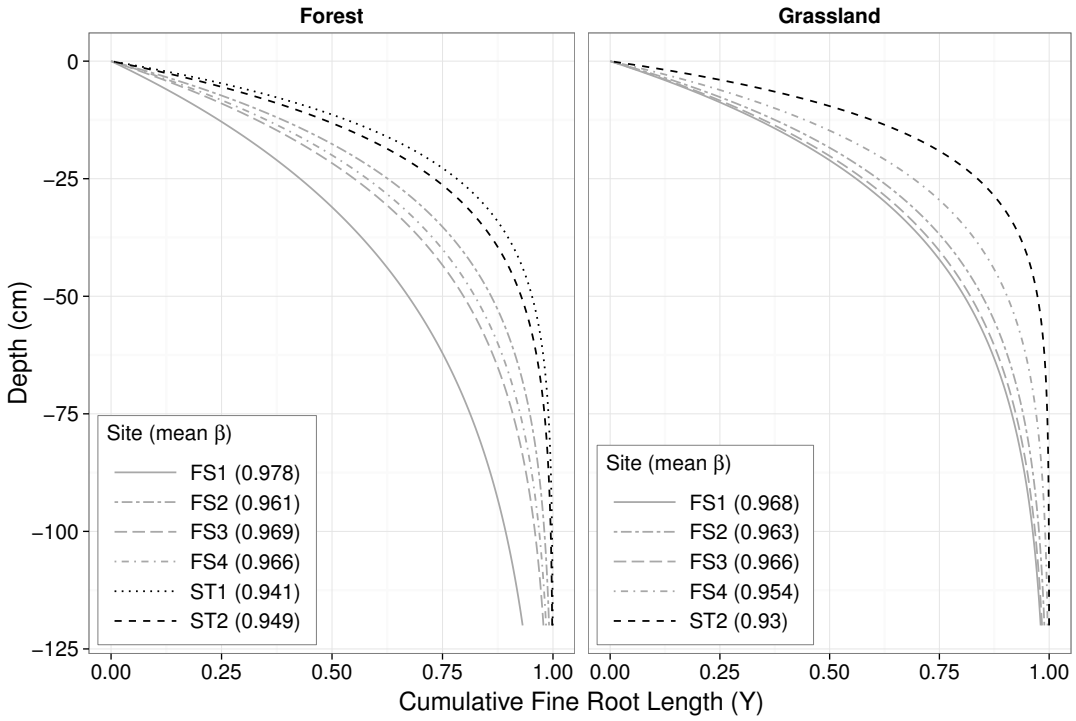


Figure 5.5: Cumulative fine root length (cumulative proportion) as a function of soil depth in forest (left panel) and grassland (right panel) for the six sites. The figure shows the differences between sites. Species are not sorted, diameter < 0.8 mm. The line was generated with the mean β (of 3 pits) from Eq. 5.5: $Y = 1 - \beta^d$ (Gale and Grigal 1987).

calculated by Jackson et al. (1997) whereas the β of our sub-taiga sites (0.941 to 0.949 in forest, overall species) were close to the mean value of boreal forest (0.943). Total fine root length and mass for the forest-steppe were comparable to those of the temperate deciduous mean value (5.4 km m^{-2} and 0.44 kg m^{-2}) and those of the sub-taiga close to boreal forest mean values (2.6 km m^{-2} and 0.23 kg m^{-2}, Jackson et al. 1997; 0.21 kg m^{-2} for roots of < 1 mm in boreal forest, Yuan and Chen 2010).

In grasslands, the β values found were higher than the mean one of temperate grassland (0.943, Jackson et al. 1997) in forest-steppe (0.946 to 0.968, Table 5.6) but in the sub-taiga our values were lower (0.911 to 0.930, Table 5.6). Total fine root length and mass were much lower than the values available in the literature for temperate grasslands (112 km m^{-2} and 0.95 kg m^{-2}, Jackson et al. 1997).

We note that the variation in β we found between bioclimatic zones of south-western Siberia approached the variation between wider terrestrial biomes shown by Jackson et al. (1997). This suggests the existence of variability among the biomes defined by these authors. Such a variability may have an importance in the evaluation of C stocks on continental or global scales since roots and their activity (e.g.

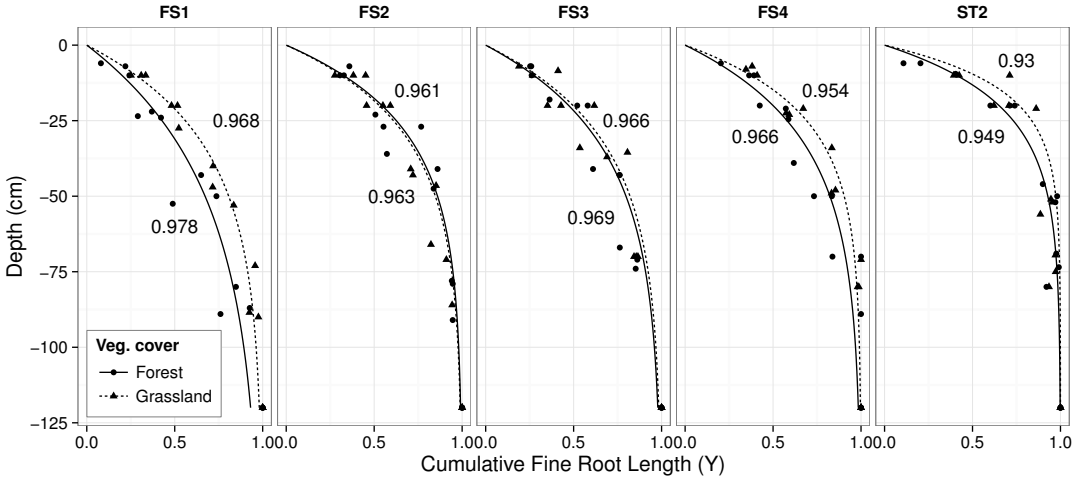


Figure 5.6: Cumulative fine root length (cumulative proportion) as a function of soil depth in forest and grassland for the six sites. The figure shows the differences between forest and grassland within sites and the quality of model fitting. Species are not sorted, diameter < 0.8 mm. Points are field measurements (3 per site and depth) and line was generated with the mean β (of 3 pits) from Eq. 5.5: $Y = 1 - \beta^d$ (Gale and Grigal 1987).

exudation) constitute C inputs. We discuss the possible causes of this variability later in the discussion.

No clear difference in aspen fine root morphological parameters (SRA, SRL) arose from the comparison of sites and zones in this study (Table 5.7). This suggests that the species did not deploy any specific morphological adaptation—or perhaps more simply that fine root morphology of aspen is not a very sensitive parameter—in the range of soil and climatic conditions of our study sites.

Vegetation type features

Fine root exploration was deeper for trees than for grass and understorey (Fig. 5.6 and 5.7, Table 5.6). This was in agreement both with field (Schenk and Jackson 2002a,b) and theoretical (e.g. Guswa 2010 on water uptake strategies) findings that herbaceous plants are more shallowly rooted than woody species. Total fine root length tended to be greater in grasslands whereas total fine root mass tended to be greater in forests (Fig. 5.2 and Table 5.6). This apparent contradiction can be attributed to differences in diameter and/or root tissue density between tree and grass roots. Our thinnest diameter class of fine roots (< 0.2 mm) represented 80–91 % of the total fine root length in grasslands whereas it represented 54–82 % of it in forests (Table C.3).

In the forest sites studied, the proportion of understorey roots in total fine root length and mass was relatively high. Understorey reached between 13 and 63 % of

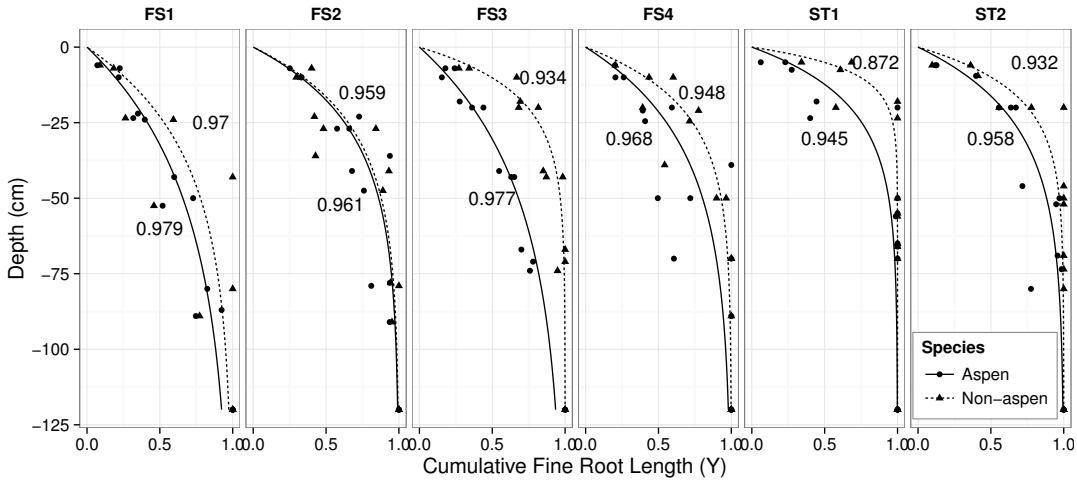


Figure 5.7: Cumulative fine root length (cumulative proportion) as a function of soil depth in forest for the six sites. The figure shows the differences between aspen and non-aspen fine root systems within forest sites and the quality of model fitting. Aspen and non-aspen (understorey vegetation) are sorted, diameter < 0.8 mm. Points are field measurements (3 per site and depth) and line was generated with the mean β (of 3 pits) from Eq. 5.5: $Y = 1 - \beta^d$ (Gale and Grigal 1987).

total fine root mass (Table C.3) whereas Finér et al. (2011a) indicated values of 20 and 31 % in temperate and boreal forest, respectively. On the study sites, no relation was found between understorey fine root length, mass or beta and LAI. This could be attributed to different species composition of the understorey strata (non-aspen vegetation either adapted to different shade conditions and/or different pedoclimatic conditions). Aspen tended to have more fine roots in the deeper layers than the understorey species and differences in vertical root distributions have been described as adaptations to reduce competition for resources (Schenk 2006). However, both understorey and aspen had their highest fine root densities in the top 30 cm of the soil, which is also where nutrient availability is highest. This pleads against the idea of a vertical niche differentiation (Gale and Grigal 1987; Yuan and Chen 2010). Rather, aspen as a tree seems able to grow deeper roots than the understorey species present in these ecosystems. Vertical rooting distributions and relationships between species on a given site may likely vary on different spatial and time scales (e.g. season, stand development stage; Kulmatiski and Beard 2013) and overlap of root distributions may not always reflect an absence of such a relationship since the uptake capacity per unit root surface of overstory trees and understorey plants is not necessarily similar (Göransson et al. 2007, 2008, 2006). Another potential explanation for the differences in rooting pattern between aspen and the understorey is that the total amounts of fine roots (length, biomass) of both aspen and understorey were quite

Table 5.7: Root morphological parameters: specific root area (SRA) and specific root length (SRL). Mean and standard error of the mean. Results presented for aspen fine roots with a diameter < 0.8 mm and for the first 3 layers sampled.

Depth	FS1		FS2		FS3		FS4		ST1		ST2	
(cm)	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
SRA ($m^2\,kg^{-1}$)												
−5	119.8	32.8	85.7	6.9	91.6	10.3	73.3	13.2	77.4	11.6	76.0	23.1
−15	110.7	10.2	93.8	6.8	197.6	72.6	92.7	7.3	78.4	22.7	95.7	15.7
−30	139.3	35.5	131.2	21.2	117.1	5.7	72.7	7.8	71.9	10.9	93.5	16.1
SRL ($m\,g^{-1}$)												
−5	14.0	5.6	9.1	1.0	9.5	1.0	7.8	1.1	6.2	0.5	7.9	2.3
−15	12.9	1.7	9.6	0.8	22.9	8.9	10.6	1.3	6.1	0.5	9.8	1.5
−30	14.7	3.5	14.3	2.2	12.0	1.0	6.3	0.8	7.5	0.6	9.9	1.7

variable between sites. More precisely, the proportion of understorey roots and their vertical distribution vary not only because of the presence of aspen but can be partly attributed to differences in the species composition of the understorey communities themselves.

5.4.2 Factors controlling patterns of fine root mass and fine root length distributions

Three types of factors are susceptible to impact fine root development in soil: the physical constraints of the environment, the availability of resources such as nutrients and water, and the interactions with other living organisms. We discuss hereafter the potential implications of physical constraints and resource availability for the fine root patterns observed in south-western Siberia.

Physical constraints to root growth

The occurrence of bedrock, high water table and soil freezing constitute three physical constraints that may impact fine root in the sites studied. While the first two may impact individual sites, strength of soil freezing might be more related to the bioclimatic zones.

We reached bedrock (a dense schist material) in FS4 around 90–100 cm. Even if a few roots were still present at the bottom of the pit (Table 5.5) further root development below 100 cm cannot be expected. In ST2 soil description revealed probable hydromorphy phenomenons: notably traces of iron oxidation in the B horizon, high water table (around 30–40 cm) observed at other sampling dates in June and October and complete saturation of the soil profile at snow-melt. A high

water table remaining for a long period in the year can be detrimental and reduce root development in deep soil layers (Imada et al. 2008). However, in the context of climate change, drier summers and earlier beginning of vegetation season could reduce the duration of high water table in this site.

Soil freezing or freeze-thaw cycles induce direct root or root-symbionts damage (Kreyling et al. 2012; Repo et al. 2014). In south-western Siberia the harshest part of the winter lasts for several months and air temperatures can drop below −40 °C (daily mean air temperatures are comprised between −14 and −18 °C in winter in our sites, Table 5.4). In such conditions, the snow-pack plays a crucial role in modulating the soil thermal regime (Dominé et al. 2007; Gouttevin et al. 2012; Qian et al. 2011; Sturm et al. 1997; Zhang 2005). With lower amounts and shorter period of snow (Table 5.4) and also probably with a snow of a higher density (Sturm et al. 1995), soils are more likely to be frozen—deeper and for longer periods—in forest-steppe than in sub-taiga. One hypothesis could be that plants growing in seasonally frozen upper-soil layers develop deeper root systems. This would maintain their integrity and lower the cost of increasing root production. Our observations fit with this hypothesis which still has to be properly tested. With the projected increases in snow depth over western Siberia (Bulygina et al. 2011, 2010, 2009; Groisman et al. 2006; Shkolnik et al. 2010), this constraint on root development in the upper soil layers might be reduced or disappear. We note that, contradicting this hypothesis or explaining why many fine roots still develop in the topsoil in forest-steppe, some experiments of soil freezing induced by snow removal resulted in higher fine root turnover while maintaining a similar fine root biomass over time (Cleavitt et al. 2008; Gaul et al. 2008; Tierney et al. 2001).

Impact of nutrient availability on root growth

Plant nutrient resources depend on organic and mineral stocks and on the processes leading to their availability. Achat et al. (2013) measured P and N stocks in two of the same study sites in south-western Siberia (FS2 and ST1). They found relatively high total and plant available P levels in the topsoil as compared with global data sets, and total N levels in the upper range of the boreal and cool-temperate life-zones but in a medium range on the global scale. These authors suggested that plant growth was more likely to be limited by N than by P in this region. While plant available P can originate both from mineral weathering and organic matter decomposition, N is available through the symbiotic fixation of atmospheric N (legumes) and/or the decomposition of dead plant material and organic matter. In this sense, N plant availability is highly dependent on microbial processes. Since organic P represented a large proportion of total P in south-western Siberia, Achat et al. (2013) suggested that microbial processes also play a significant role in P availability. This might explain partly the relatively high density of fine roots observed in the topsoil since

both organic matter and microbial decomposers are concentrated there.

Within the same geographical area, modifications of fine root densities (higher stocks: Achat et al. 2008; Finér et al. 2007; Helmisaari et al. 2007; Keyes and Grier 1981; Vogt et al. 1996) and morphological plasticity (higher SRL and SRA: Bakker et al. 2009; Maurice et al. 2010; Ostonen et al. 2007; Ostonen et al. 1999) have been observed in the most fertile or in fertilized sites. In south-western Siberia, nutrient availability might be sensitive to climatic conditions since the metabolic activity of microbial decomposers is partly controlled by temperature and precipitation (Davidson and Janssens 2006; Pregitzer et al. 2000). With higher temperatures at wintertime, due to higher snow cover, one may expect higher nutrient availability at the beginning of the vegetation season in sub-taiga and no need for development of deeper fine roots to maintain the demand. Through the same mechanism, climate change is likely to indirectly modulate fine root profiles. Whether fine roots will invest more in the top soil (through increased densities), in deeper horizons (exploration of new horizons) or adapt morphologically, will depend on the needs of the plants for nutrients and water and how nutrient and water availability are distributed in the soil profile.

Impact of water availability on root growth

Precipitation regime and soil water storage capacity are two key components for water availability. Total precipitation has been widely correlated with fine root densities but differences among studies were rather diverging (Finér et al. 2007; Leuschner and Hertel 2003; Yuan and Chen 2010) suggesting other environmental controls and seasonal dynamics of soil water content have to be taken into account.

On average, mean annual precipitation is relatively low in south-western Siberia (Table 5.4) but is concentrated on the growing season (peak in July). We monitored soil moisture content in FS1 and ST2 and explored data archived in the International Soil Moisture Network (data not shown). Soil moisture dropped down at summertime with generally much drier conditions in forest-steppe than in sub-taiga and, while soil was regularly re-saturated at autumn in sub-taiga, the snow-melt (in April–May) was of great importance for soil water recharge in forest-steppe. This can be related to lower total precipitation in forest-steppe, higher evapo-transpiration in summer, and also locally lower water storage capacities due to soil properties (for example, FS1 is located on the top of a 80 m loess plateau with a relatively high drainage lowering the opportunities to saturate the profile).

Schenk and Jackson (2002b) reported deeper fine root profiles in drier ecosystems on the global scale. We found a similar pattern on a regional scale since fine root profiles were deeper in forest-steppe than in sub-taiga. In accord with Hertel et al. (2013), our driest sites (forest-steppe) exhibited a higher total fine root mass than the wetter ones (sub-taiga). However, other studies reported the contrary (Meier and Leuschner 2008; Nisbet and Mullins 1986). Interestingly, both (Meier and Leuschner

2008) and (Hertel et al. 2013) conducted their studies in similar climate contexts in Germany but in contrasted soil conditions (bedrock, pH, base saturation, nutrients, etc.). Hertel et al. (2013) also reported that the strength of the precipitation effects on fine roots biomass and productivity was modulated by soil texture.

An increase in winter precipitation—thus a higher input of water into the soil at snow-melt—may constitute an increased water reserve for the ongoing growing season in the sites which are not currently saturated after snow-melt and/or with a capacity to store more water in the deeper layers. Typically, we might expect forest-steppe to benefit from such a changing regime in winter precipitation but not sub-taiga. Of course, other seasonal dynamics would modulate this effect and since more severe droughts are expected in forest-steppe areas it is impossible to infer the final status given the data discussed here. Variations in soil moisture content can also interfere with microbial activity and thus on nutrient availability.

5.5 Conclusion

This study of fine root length, mass and distribution within the soil profile in south-western Siberia revealed patterns related to bioclimatic zones and vegetation cover type. Length, mass and depth of fine roots were higher in forest-steppe than in sub-taiga. Within the same site, forests had deeper roots than grasslands and trees exhibited deeper roots than understorey in the forests. No morphological adaptations occurred for aspen roots. These patterns can be related to contrasting pedoclimatic conditions.

We discussed two types of factors that could be involved in the control of these fine root patterns: physical constraints to root development and the availability of resources (nutrients and water). To summarize, in forest-steppe climatic conditions are drier and the snow-melt is of great importance for recharging soil with water, soils are more frequently and more severely subjected to soil freezing at wintertime, litter decomposition seems to occur more slowly suggesting the source of nutrients could be both mineral (over the the whole soil profile) and organic (in the topsoil). We hypothesize the combination of these factors plays for deeper fine root systems. On the contrary, the climatic conditions of the sub-taiga are wetter, soil is frequently saturated with water, protected from freezing in winter and litter decomposition may be faster, suggesting the importance of mineralization for nutrient availability. We hypothesize the combination of these factors plays for shallower fine root profiles. However, the confrontation of additional data on soil properties (such as pH, granulometry and nutrient content) and soil water budget dynamics are required to better understand fine root patterns in south-western Siberia and predict their potential evolution with global change, which is often predicted to permit higher primary productivity (Norby et al. 2005). In particular, a deepening of root systems

may occur with the increase of atmospheric CO_2 levels (Iversen 2010) and with the increasing length of the growing season (Majdi and Öhrvik 2004). Such a deepening could impact C stock, especially in deep soil horizons, because root production constitutes inputs of fresh C and may induce destabilization of old C by priming effect.

Acknowledgements

We thank D. L. Achat, the editor and three anonymous reviewers for carefully reading and commenting earlier versions of this manuscript. We are grateful to all the people who helped on the field in July 2013, notably to A. Bashuk and J. Petrashova. Botanical descriptions were performed by N. Gaberman, N. Kolosov and A. Stupak. J.-L. Dupouey and F. Gérémia provided support for tree cores analysis. Climate data were provided by RIHMI-WDC, we particularly thank O. Bulygina for the preparation of relevant data sets. The project was funded by INRA Métaprogramme ACCAF and ERA.Net RUS.

References

Achat, D. L., Bakker, M. R., Augusto, L., Derrien, D., Gallegos, N., Lashchinskiy, N., Milin, S., Nikitich, P., Raudina, T., Rusalimova, O., Zeller, B., and Barsukov, P. (2013). Phosphorus status of soils from contrasting forested ecosystems in southwestern Siberia: effects of microbiological and physicochemical properties. *Biogeosciences* 10.2, 733–752. DOI: 10.5194/bg-10-733-2013.

Achat, D., Bakker, M., and Trichet, P. (2008). Rooting patterns and fine root biomass of Pinus pinaster assessed by trench wall and core methods. *Journal of Forest Research* 13 (3), 165–175. DOI: 10.1007/s10310-008-0071-y.

Bakker, M., Augusto, L., and Achat, D. (2006). Fine root distribution of trees and understory in mature stands of maritime pine (Pinus pinaster) on dry and humid sites. *Plant and Soil* 286 (1-2), 37–51. DOI: 10.1007/s11104-006-9024-4.

Bakker, M., Jolicoeur, E., Trichet, P., Augusto, L., Plassard, C., Guinberteau, J., and Loustau, D. (2009). Adaptation of fine roots to annual fertilization and irrigation in a 13-year-old Pinus pinaster stand. *Tree Physiology* 29.2, 229–238. DOI: 10.1093/treephys/tpn020.

Berg, B. (1984). Decomposition of root litter and some factors regulating the process: Long-term root litter decomposition in a scots pine forest. *Soil Biology and Biochemistry* 16.6, 609–617. DOI: http://dx.doi.org/10.1016/0038-0717(84)90081-6.

Bergen, K. M., Hitztaler, S. K., Kharuk, V. I., Krankina, O. N., Loboda, T. V., Zhao, T., Shugart, H. H., and Sun, G. (2012). Human dimensions of environmental change in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*, 251–302. DOI: 10.1007/978-94-007-4569-8_7.

Braun-Blanquet, J., Conard, H. S., and Fuller, G. D. (1932). *Plant sociology—the study of plant communities—authorized English translation of Pflanzensoziologie, by Dr. J. Braun-Blanquet. Translated, revised and edited by George D. Fuller and Henry S. Conard.* McGraw-Hill book company, inc. DOI: 10.5962/bhl.title.7161.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Korshunova, N. N. (2011). Changes in snow cover characteristics over Northern Eurasia since 1966. *Environmental Research Letters* 6.4, 045204. DOI: 10.1088/1748-9326/6/4/045204.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Radionov, V. F. (2010). Snow cover basal ice layer changes over Northern Eurasia since 1966. *Environmental Research Letters* 5.1, 015004. DOI: 10.1088/1748-9326/5/1/015004.

Bulygina, O. N., Razuvaev, V. N., and Korshunova, N. N. (2009). Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters* 4.4, 045026. DOI: 10.1088/1748-9326/4/4/045026.

Cabestan, J.-P., Colin, S., Facon, I., and Meidan, M. (2008). *La Chine et la Russie : Entre convergences et méfiance.* UNICOMM. 274 pp.

Cleavitt, N. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Henry, K. S., and Driscoll, C. T. (2008). Effects of soil freezing on fine roots in a northern hardwood forest. *Canadian Journal of Forest Research* 38.1, 82–91. DOI: 10.1139/x07-133.

Davidson, E. A. and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440.7081, 165–173. DOI: 10.1038/nature04514.

Dominé, F., Taillandier, A., Houdier, S., Parrenin, F., Simpson, W., and Douglas, T. (2007). Interactions between snow metamorphism and climate: physical and chemical aspects. In: *Physics and Chemistry of Ice*, 27–46.

Finér, L., Helmisaari, H.-S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, T., Godbold, D., Grebenc, T., Konôpka, B., Kraigher, H., Möttönen, M.-R., Ohashi, M., Oleksyn, J., Ostonen, I., Uri, V., and Vanguelova, E. (2007). Variation in fine root biomass of three European tree species: Beech (Fagus sylvatica L.), Norway spruce (Picea abies L. Karst.), and Scots pine (Pinus sylvestris L.) *Plant Biosystems* 141.3, 394–405. DOI: 10.1080/11263500701625897.

Finér, L., Ohashi, M., Noguchi, K., and Hirano, Y. (2011a). Factors causing variation in fine root biomass in forest ecosystems. *Forest Ecology and Management* 261.2, 265–277. DOI: 10.1016/j.foreco.2010.10.016.

Finér, L., Ohashi, M., Noguchi, K., and Hirano, Y. (2011b). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* 262.11, 2008–2023. DOI: 10.1016/j.foreco.2011.08.042.

Gale, M. R. and Grigal, D. F. (1987). Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research* 17.8, 829–834. DOI: 10.1139/x87-131.

Gaul, D., Hertel, D., and Leuschner, C. (2008). Effects of experimental soil frost on the fine-root system of mature Norway spruce. *Journal of Plant Nutrition and Soil Science* 171.5, 690–698. DOI: 10.1002/jpln.200700284.

Gill, R. A. and Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147.1, 13–31. DOI: 10.1046/j.1469-8137.2000.00681.x.

Gonzalez, M., Augusto, L., Gallet-Budynek, A., Xue, J., Yauschew-Raguenes, N., Guyon, D., Trichet, P., Delerue, F., Niollet, S., Andreasson, F., Achat, D. L., and Bakker, M. R. (2013). Contribution of understory species to total ecosystem aboveground and belowground biomass in temperate Pinus pinaster Ait. forests. *Forest Ecology and Management* 289, 38–47. DOI: 10.1016/j.foreco.2012.10.026.

Göransson, H., Fransson, A.-M., and Jönsson-Belyazid, U. (2007). Do oaks have different strategies for uptake of N, K and P depending on soil depth? *Plant and Soil* 297.1-2, 119–125. DOI: 10.1007/s11104-007-9325-2.

Göransson, H., Ingerslev, M., and Wallander, H. (2008). The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature Quercus robur, Fagus sylvatica and Picea abies stands. *Plant and Soil* 306.1-2, 129–137. DOI: 10.1007/s11104-007-9524-x.

Göransson, H., Wallander, H., Ingerslev, M., and Rosengren, U. (2006). Estimating the relative nutrient uptake from different soil depths in Quercus robur, Fagus sylvatica and Picea abies. *Plant and Soil* 286.1-2, 87–97. DOI: 10.1007/s11104-006-9028-0.

Gordov, E. P. and Vaganov, E. A. (2010). Siberia integrated regional study: multidisciplinary investigations of the dynamic relationship between the Siberian environment and global climate change. *Environmental Research Letters* 5.1, 015007. DOI: 10.1088/1748-9326/5/1/015007.

Gouttevin, I., Menegoz, M., Dominé, F., Krinner, G., Koven, C., Ciais, P., Tarnocai, C., and Boike, J. (2012). How the insulating properties of snow affect soil carbon distribution in the continental pan-Arctic area. *Journal of Geophysical Research* 117.G2. DOI: 10.1029/2011jg001916.

Groisman, P. Y., Knight, R. W., Razuvaev, V. N., Bulygina, O. N., and Karl, T. R. (2006). State of the ground: Climatology and changes during the past 69 Years over Northern Eurasia for a rarely used measure of snow cover and frozen land. *Journal of Climate* 19.19, 4933–4955. DOI: 10.1175/JCLI3925.1.

Groisman, P. and Soja, A. J. (2009). Ongoing climatic change in Northern Eurasia: justification for expedient research. *Environmental Research Letters* 4.4, 045002. DOI: 10.1088/1748-9326/4/4/045002.

Guo, D., Li, H., Mitchell, R. J., Han, W., Hendricks, J. J., Fahey, T. J., and Hendrick, R. L. (2008). Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* 177.2, 443–456. DOI: 10.1111/j.1469-8137.2007.02242.x.

Guswa, A. J. (2010). Effect of plant uptake strategy on the water-optimal root depth. *Water Resources Research* 46.9. DOI: 10.1029/2010wr009122.

Hansson, K., Helmisaari, H.-S., Sah, S. P., and Lange, H. (2013). Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. *Forest Ecology and Management* 309, 58–65. DOI: 10.1016/j.foreco.2013.01.022.

Helmisaari, H.-S., Makkonen, K., Kellomäki, S., Valtonen, E., and Mälkönen, E. (2002). Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *Forest Ecology and Management* 165.1–3, 317–326. DOI: http://dx.doi.org/10.1016/S0378-1127(01)00648-X.

Helmisaari, H.-S., Derome, J., Nojd, P., and Kukkola, M. (2007). Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. *Tree Physiology* 27.10, 1493–1504. DOI: 10.1093/treephys/27.10.1493.

Hendrick, R. L. and Pregitzer, K. S. (1993). The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Canadian Journal of Forest Research* 23.12, 2507–2520. DOI: 10.1139/x93-312.

Hendricks, J. J., Hendrick, R. L., Wilson, C. A., Mitchell, R. J., Pecot, S. D., and Guo, D. (2006). Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology* 94.1, 40–57. DOI: 10.1111/j.1365-2745.2005.01067.x.

Hertel, D., Strecker, T., Müller-Haubold, H., and Leuschner, C. (2013). Fine root biomass and dynamics in beech forests across a precipitation gradient - is optimal resource partitioning theory applicable to water-limited mature trees? *Journal of Ecology* 101.5, 1183–1200. DOI: 10.1111/1365-2745.12124.

Imada, S., Yamanaka, N., and Tamai, S. (2008). Water table depth affects Populus alba fine root growth and whole plant biomass. *Functional Ecology* 22.6, 1018–1026. DOI: 10.1111/j.1365-2435.2008.01454.x.

IUSS Working Group WRB (2014). *World Reference Base for Soil Resources 2014 - International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106.* FAO.

Iversen, C. M. (2010). Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. *New Phytologist* 186.2, 346–357. DOI: 10.1111/j.1469-8137.2009.03122.x.

Iversen, C. M. (2014). Using root form to improve our understanding of root function. *New Phytologist* 203.3, 707–709. DOI: 10.1111/nph.12902.

Jackson, R. B., Mooney, H. A., and Schulze, E.-. D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* 94.14, 7362–7366. DOI: 10.1073/pnas.94.14.7362.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J. (2012). Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. *Ecology and Evolution* 2.3, 593–614. DOI: 10.1002/ece3.85.

Joslin, J. D. and Henderson, G. S. (1987). Organic matter and nutrients associated with fine root turnover in a white oak stand. *Forest Science* 33.2, 330–346.

Joslin, J. D., Wolfe, M. H., and Hanson, P. J. (2000). Effects of altered water regimes on forest root systems. *New Phytologist* 147.1, 117–129. DOI: 10.1046/j.1469-8137.2000.00692.x.

Kalyn, A. and Rees, K. V. (2006). Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan.

Agricultural and Forest Meteorology 140.1-4, 236–243. DOI: 10.1016/j.agrformet.2005.08.019.

Keel, S. G., Campbell, C. D., Högberg, M. N., Richter, A., Wild, B., Zhou, X., Hurry, V., Linder, S., Näsholm, T., and Högberg, P. (2012). Allocation of carbon to fine root compounds and their residence times in a boreal forest depend on root size class and season. *New Phytologist* 194.4, 972–981. DOI: 10.1111/j.1469-8137.2012.04120.x.

Keyes, M. R. and Grier, C. C. (1981). Above- and below-ground net production in 40-year-old douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research* 11.3, 599–605. DOI: 10.1139/x81-082.

King, J. S., Albaugh, T. J., Allen, H. L., Buford, M., Strain, B. R., and Dougherty, P. (2002). Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytologist* 154.2, 389–398. DOI: 10.1046/j.1469-8137.2002.00393.x.

Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H., and Guo, D. (2014). Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* 203.3, 863–872. DOI: 10.1111/nph.12842.

Kreyling, J., Peršoh, D., Werner, S., Benzenberg, M., and Wöllecke, J. (2012). Short-term impacts of soil freeze-thaw cycles on roots and root-associated fungi of Holcus lanatus and Calluna vulgaris. *Plant and Soil* 353 (1-2), 19–31. DOI: 10.1007/s11104-011-0970-0.

Kulmatiski, A. and Beard, K. (2013). Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia* 171.1, 25–37. DOI: 10.1007/s00442-012-2390-0.

Leppälammi-Kujansuu, J., Aro, L., Salemaa, M., Hansson, K., Kleja, D. B., and Helmisaari, H.-S. (2014). Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. *Forest Ecology and Management* 326, 79–90. DOI: 10.1016/j.foreco.2014.03.039.

Leuschner, C. and Hertel, D. (2003). Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. In: *Progress in Botany*, 405–438. DOI: 10.1007/978-3-642-55819-1_16.

Majdi, H. and Öhrvik, J. (2004). Interactive effects of soil warming and fertilization on root production, mortality, and longevity in a Norway spruce stand in Northern Sweden. *Global Change Biology* 10.2, 182–188. DOI: 10.1111/j.1365-2486.2004.00733.x.

Maurice, J., Laclau, J.-P., Re, D. S., Moraes Gonçalves, J. L. de, Nouvellon, Y., Bouillet, J.-P., Stape, J. L., Ranger, J., Behling, M., and Chopart, J.-L. (2010). Fine root isotropy in Eucalyptus grandis plantations. Towards the prediction of root length densities from root counts on trench walls. *Plant and Soil* 334.1-2, 261–275. DOI: 10.1007/s11104-010-0380-8.

McCormack, M. L., Adams, T. S., Smithwick, E. A. H., and Eissenstat, D. M. (2014). Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95.8, 2224–2235. DOI: 10.1890/13-1942.1.

McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., Helmisaari, H.-S., Hobbie, E. A., Iversen, C. M., Jackson, R. B., Leppälammi-Kujansuu, J., Norby, R. J., Phillips, R. P., Pregitzer, K. S., Pritchard, S. G., Rewald, B., and Zadworny, M.

(2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207.3, 505–518. DOI: 10.1111/nph.13363.

McCormack, M. L., Eissenstat, D. M., Prasad, A. M., and Smithwick, E. A. H. (2013). Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biology* 19.6, 1697–1708. DOI: 10.1111/gcb.12163.

McCormack, M. L. and Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science* 5. DOI: 10.3389/fpls.2014.00205.

Meier, I. C. and Leuschner, C. (2008). Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biology* 14.9, 2081–2095. DOI: 10.1111/j.1365-2486.2008.01634.x.

Moore, P. T., Miegroet, H. V., and Nicholas, N. S. (2007). Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. *Canadian Journal of Forest Research* 37.12, 2689–2700. DOI: 10.1139/x07-115.

Nisbet, T. R. and Mullins, C. E. (1986). A comparison of live and dead fine root weights in stands of Sitka spruce in contrasting soil water regimes. *Canadian Journal of Forest Research* 16.2, 394–397. DOI: 10.1139/x86-068.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R. (2005). Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* 102.50, 18052–18056. DOI: 10.1073/pnas.0509478102.

Ostonen, I., Lohmus, K., Helmisaari, H.-S., Truu, J., and Meel, S. (2007). Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. *Tree Physiology* 27.11, 1627–1634. DOI: 10.1093/treephys/27.11.1627.

Ostonen, I., Lõhmus, K., and Lasn, R. (1999). The role of soil conditions in fine root ecomorphology in Norway spruce (Picea abies (L.) Karst.) *Plant and Soil* 208.2, 283–292. DOI: 10.1023/A:1004552907597.

Pierret, A., Moran, C. J., and Doussan, C. (2005). Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots. *New Phytologist* 166.3, 967–980. DOI: 10.1111/j.1469-8137.2005.01389.x.

Pregitzer, K. S., Laskowski, M. J., Burton, A. J., Lessard, V. C., and Zak, D. R. (1998). Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* 18.10, 665–670. DOI: 10.1093/treephys/18.10.665.

Pregitzer, K. S. (2002). Fine roots of trees - a new perspective. *New Phytologist* 154.2, 267–270. DOI: 10.1046/j.1469-8137.2002.00413_1.x.

Pregitzer, K. S., DeForest, J. L., Burton, A. J., Allen, M. F., Ruess, R. W., and Hendrick, R. L. (2002). Fine root architecture of nine North American trees. *Ecological Monographs* 72.2, 293. DOI: 10.2307/3100029.

Pregitzer, K. S., King, J. S., Burton, A. J., and Brown, S. E. (2000). Responses of tree fine roots to temperature. *New Phytologist* 147.1, 105–115. DOI: 10.1046/j.1469-8137.2000.00689.x.

Pregitzer, K. S., Kubiske, M. E., Yu, C. K., and Hendrick, R. L. (1997). Relationships among root branch order, carbon, and nitrogen in four temperate species. *Oecologia* 111.3, 302–308. DOI: 10.1007/s004420050239.

Qian, B., Gregorich, E. G., Gameda, S., Hopkins, D. W., and Wang, X. L. (2011). Observed soil temperature trends associated with climate change in Canada. *Journal of Geophysical Research* 116.D2. DOI: 10.1029/2010jd015012.

R Core Team (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Repo, T., Sirkiä, S., Heinonen, J., Lavigné, A., Roitto, M., Koljonen, E., Sutinen, S., and Finér, L. (2014). Effects of frozen soil on growth and longevity of fine roots of Norway spruce. *Forest Ecology and Management* 313, 112–122. DOI: 10.1016/j.foreco.2013.11.002.

Richter, D. D., Markewitz, D., Trumbore, S. E., and Wells, C. G. (1999). Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature* 400.6739, 56–58. DOI: 10.1038/21867.

Ruess, R. W., Hendrick, R. L., Burton, A. J., Pregitzer, K. S., Sveinbjornssön, B., Allen, M. F., and Maurer, G. E. (2003). Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs* 73.4, 643–662. DOI: 10.1890/02-4032.

Schenk, H. J. (2006). Root competition: beyond resource depletion. *Journal of Ecology* 94.4, 725–739. DOI: 10.1111/j.1365-2745.2006.01124.x.

Schenk, H. J. and Jackson, R. B. (2002a). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90.3, 480–494. DOI: 10.1046/j.1365-2745.2002.00682.x.

Schenk, H. J. and Jackson, R. B. (2002b). The global biogeography of roots. *Ecological Monographs* 72.3, 311. DOI: 10.2307/3100092.

Shepashenko, D., Shvidenko, A., and Nilsson, S. (1998). Phytomass (live biomass) and carbon of Siberian forests. *Biomass and Bioenergy* 14.1, 21–31. DOI: 10.1016/s0961-9534(97)10006-x.

Shiklomanov, A. I. and Lammers, R. B. (2009). Record Russian river discharge in 2007 and the limits of analysis. *Environmental Research Letters* 4.4, 045015. DOI: 10.1088/1748-9326/4/4/045015.

Shkolnik, I. M., Nadyozhina, E. D., Pavlova, T. V., Molkentin, E. K., and Semioshina, A. A. (2010). Snow cover and permafrost evolution in Siberia as simulated by the MGO regional climate model in the 20th and 21st centuries. *Environmental Research Letters* 5.1, 015005. DOI: 10.1088/1748-9326/5/1/01500510.1088/1748-9326/5/1/015005.

Smith, S. W., Woodin, S. J., Pakeman, R. J., Johnson, D., and Wal, R. van der (2014). Root traits predict decomposition across a landscape-scale grazing experiment. *New Phytologist* 203.3, 851–862. DOI: 10.1111/nph.12845.

Smithwick, E. A., Lucash, M. S., McCormack, M. L., and Sivandran, G. (2014). Improving the representation of roots in terrestrial models. *Ecological Modelling* 291, 193–204. DOI: 10.1016/j.ecolmodel.2014.07.023.

Snegur, J. (2006). Sibérie russe, Sibérie chinoise ? *Outre-Terre* 15 (2), 279–286. DOI: 10.3917/oute.015.0279.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S., and Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56.3–4, 274–296. DOI: 10.1016/j.gloplacha.2006.07.028.

Steinaker, D. F., Wilson, S. D., and Peltzer, D. A. (2010). Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology* 16.8, 2241–2251. DOI: 10.1111/j.1365-2486.2009.02065.x.

Sturm, M., Holmgreen, J., König, M., and Morris, K. (1997). The thermal conductivity of seasonal snow. *Journal of Glaciology* 43.143, 26–41.

Sturm, M., Holmgren, J., and Liston, G. E. (1995). A seasonal snow cover classification system for local to global applications. *Journal of Climate* 8.5, 1261–1283. DOI: 10.1175/1520-0442(1995)008<1261:ASSCCS>2.0.CO;2.

Taylor, B. N., Beidler, K. V., Cooper, E. R., Strand, A. E., and Pritchard, S. G. (2013). Sampling volume in root studies: the pitfalls of under-sampling exposed using accumulation curves. *Ecology Letters* 16.7, 862–869. DOI: 10.1111/ele.12119.

Tchebakova, N. M., Parfenova, E. I., Lysanova, G. I., and Soja, A. J. (2011). Agroclimatic potential across central Siberia in an altered twenty-first century. *Environmental Research Letters* 6.4, 045207. DOI: 10.1088/1748-9326/6/4/045207.

Tchebakova, N. M., Parfenova, E., and Soja, A. J. (2009). The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4.4, 045013. DOI: 10.1088/1748-9326/4/4/045013.

Tchebakova, N. M., Rehfeldt, G. E., and Parfenova, E. I. (2010). From vegetation zones to climatypes: Effects of climate warming on Siberian ecosystems. In: *Permafrost Ecosystems. Siberian Larch Forests*. Chap. 22, 427–447.

Tennant, D. (1975). A test of a modified line intersect method of estimating root length. *Journal of Ecology* 63.3, 995–1001. DOI: 10.2307/2258617.

Tierney, G., Fahey, T., Groffman, P., Hardy, J., Fitzhugh, R., and Driscoll, C. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56.2, 175–190. DOI: 10.1023/A:1013072519889.

Valenzuela-Estrada, L. R., Vera-Caraballo, V., Ruth, L. E., and Eissenstat, D. M. (2008). Root anatomy, morphology, and longevity among root orders in Vaccinium corymbosum (Ericaceae). *American Journal of Botany* 95.12, 1506–1514. DOI: 10.3732/ajb.0800092.

Vogt, K., Vogt, D., and Bloomfield, J. (1998). Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil* 200 (1), 71–89. DOI: 10.1023/A:1004313515294.

Vogt, K., Vogt, D., Palmiotto, P., Boon, P., O'Hara, J., and Asbjornsen, H. (1996). Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant and Soil* 187 (2), 159–219. DOI: 10.1007/BF00017088.

Warren, J. M., Hanson, P. J., Iversen, C. M., Kumar, J., Walker, A. P., and Wullschleger, S. D. (2015). Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations. *New Phytologist* 205.1, 59–78. DOI: 10.1111/nph.13034.

Wells, C. E. and Eissenstat, D. M. (2001). Marked differences in survivorship among apple roots of different diameters. *Ecology* 82.3, 882. DOI: 10.2307/2680206.

Whigham, D. F. (2004). Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology, Evolution, and Systematics* 35.1, 583–621. DOI: 10.1146/annurev.ecolsys.35.021103.105708.

Yarie, J. (1980). The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. *Ecology* 61.6, 1498. DOI: 10.2307/1939057.

Yuan, Z. Y. and Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. *Critical Reviews in Plant Sciences* 29.4, 204–221. DOI: 10.1080/07352689.2010.483579.

Yuan, Z. Y. and Chen, H. Y. H. (2012a). A global analysis of fine root production as affected by soil nitrogen and phosphorus. *Proceedings of the Royal Society B: Biological Sciences* 279.1743, 3796–3802. DOI: 10.1098/rspb.2012.0955.

Yuan, Z. Y. and Chen, H. Y. H. (2012b). Fine root dynamics with stand development in the boreal forest. *Functional Ecology* 26.4, 991–998. DOI: 10.1111/j.1365-2435.2012.02007.x.

Zhang, T. (2005). Influence of the seasonal snow cover on the ground thermal regime: An overview. *Reviews of Geophysics* 43.4. DOI: 10.1029/2004rg000157.

Chapter 6

What is the P value of Siberian soils?

A modified version of this chapter has been published with the following reference: Brédoire, F., Bakker, M. R., Augusto, L., Barsukov, P. A., Derrien, D., Nikitich, P., Rusalimova, O., Zeller, B., and Achat, D. L. (2016a). What is the P value of Siberian soils? Soil phosphorus status in south-western Siberia and comparison with a global data set. *Biogeosciences* 13.8, 2493–2509. DOI: 10.5194/bg-13-2493-2016

Abstract

Climate change is particularly strong in Northern Eurasia and substantial ecological changes are expected in this extensive region. The reshaping and migration northwards of bioclimatic zones may offer opportunities for agricultural development in western and central Siberia. However, the bioclimatic vegetation models currently employed for projections still do not consider soil fertility, in spite of this being highly critical for plant growth. In the present study, we surveyed the phosphorus (P) status in the south-west of Siberia where soils are developed on loess parent material. We selected six sites differing in pedoclimatic conditions and the soil was sampled at different depths down to 1 m in aspen (*Populus tremula* L.) forest as well as in grassland areas. The P status was assessed by conventional methods and by isotope dilution kinetics. We found that P concentrations and stocks, as well as their distribution through the soil profile, were fairly homogeneous on the regional scale studied, although there were some differences between sites (particularly in organic P). The young age of the soils, together with slow kinetics of soil formation processes have probably not yet resulted in a sufficiently wide range of soil physico-chemical conditions to observe a more diverging P status. The comparison of our data set with similar vegetation contexts on the global scale revealed that the soils of south-western Siberia and more generally of Northern Eurasia, often have (very) high levels of total, organic and inorganic P. The amount of plant-available P in topsoils, estimated by the isotopically exchangeable phosphate ions, was not particularly high but was intermediate on the global scale. However, large stocks of plant-available P are stored in subsurface layers which currently have low fine-root exploration intensities. These results suggest that the P resource is unlikely to con-

strain vegetation growth and agricultural development under the present conditions or in the near future.

6.1 Introduction

Occupying about 10 million km^2 (6.7 % of global terrestrial land), Siberia has a paramount influence because ecological processes occurring here can have an impact on the global scale. Ranging from latitudes 45 to 75 °N, it covers several bioclimatic zones, from south to north: steppe, forest-steppe, sub-taiga, southern taiga, middle taiga, northern taiga, forest tundra and tundra. As the global climate change signal is particularly strong in Northern Eurasia (IPCC 2013), substantial reshaping of ecosystems is ongoing in the region. The expected increase in average air temperatures will be responsible for longer vegetation growing seasons and frost-free periods, for the melt of permafrost in northern areas and for the modification of soil freeze–thaw cycles in southern areas (Groisman et al. 2012). The intensity and distribution of precipitation may change, resulting in differences in fire and hydrological regimes (Shiklomanov and Lammers 2009; Shkolnik et al. 2010; Soja et al. 2007). These altered physical conditions are expected to modify the composition of the plant communities and the bioclimatic zones of Siberia have been predicted to shift northwards and their relative size to change (Jiang et al. 2012; Shuman et al. 2015; Soja et al. 2007; Tchebakova et al. 2009, 2010). In particular, the area occupied by steppe and forest-steppe would increase at the expense of taiga zones. These modifications of ecosystem features may result in alternative land uses (Bergen et al. 2012; Kicklighter et al. 2014). Notably, under future climatic conditions, cropping of new species will be possible, or existing species may be used in more extensive zones than at present in the southern parts of Western and Central Siberia (Kicklighter et al. 2014; Tchebakova et al. 2011). Primary productivity may be enhanced due to a "fertilization" effect induced by higher CO_2 levels in the air (Mooney et al. 1991; Norby et al. 2005; Schimel 1995) along with longer periods sustaining plant growth. However, such projections lack the consideration of other important drivers of plant productivity such as the availability of resources like nutrients and water in soils (Fernández-Martínez et al. 2014; He and Dijkstra 2014; Oren et al. 2001; Reich et al. 2014, 2006a,b; van Groenigen et al. 2006). Even though there is an increasing interest in the study of Siberian ecosystems, functional ecological data remain sparse in the international literature (Gordov and Vaganov 2010; Groisman and Soja 2009).

In the domain of biogeochemistry, knowledge about the status of the major nutrients is lacking, and potentially misleading assumptions could be made for Siberia. Together with nitrogen (N), phosphorus (P) is frequently a limiting resource for primary production on the ecosystem scale (Elser et al. 2007; Harpole et al. 2011), but it is often considered that P is not the main limiting factor in northern ecosystems

(Hedin 2004; Reich and Oleksyn 2004). Also, P fertilization in agriculture is rarely practised in Siberia, if at all. However, a reconsideration of such a paradigm might be necessary in the context of global change. In fact, the increase in atmospheric CO_2 concentrations and N deposition, which is in general stronger and faster than any P input, is modifying the CNP stoichiometry of ecosystems (Peñuelas et al. 2013). As a consequence, a progressive shift from N limitation to P limitation or N–P co-limitation can occur (Ågren et al. 2012; Peñuelas et al. 2012; Vitousek et al. 2010). These modifications of biogeochemical cycling on global and regional scales will participate in the way ecosystem reshaping is driven, for example through the modification of plant communities as they adapt to new stoichiometric constraints (Güsewell 2004). It may also have consequences for agricultural potential on these scales.

In addition, the global resources of P that are used for mineral fertilizer production are limited (Cooper et al. 2011; Cordell et al. 2009). Therefore, enhancing our understanding of P cycles and managing them appropriately on the global scale is highly relevant (Cordell et al. 2011; MacDonald et al. 2011) since modern terrestrial P cycling is dominated by human activities (Filippelli 2008). One solution which would help to restrict the use of primary P resources would be the development of cropping systems in areas where the soils contain sufficient plant-available P to prevent the (massive) use of P fertilizers. In this perspective, parts of Siberia are expected to become climatically more suitable for agriculture. Assessing the P status of these Siberian regions is thus of relevance, and this was the main goal of our study.

In the present study, we aimed to identify the P status of the soils of SW Siberia, a region characterized by different types of soil along a north–south climatic gradient. We addressed the following questions: (1) How is the P stock structured, in terms of pools and with depth, in the soils of SW Siberia? (2) Which environmental factors control this P status? (3) How can we qualify this P status in comparison with a range of contrasting pedoclimatic conditions on the global scale? To do this, we selected six sites with contrasting pedoclimatic conditions in SW Siberia and presenting two characteristic vegetation covers: aspen (*Populus tremula*) forests and grasslands. We quantified total P, organic P, phosphate ions in solution and diffusive phosphate ions as a function of time in the soils from these sites. Classical soil analysis methods were combined with an isotopic dilution kinetics method. The size of P pools assessed at Siberian sites were compared with a global data set compiled from 236 references.

Table 6.1: Main characteristics of the study sites. Additional information is provided in Tables D.1 to D.3.

Site ID	BAR	CHE	KRA	SAE	SAW	TOM
Geographical characteristics						
Name[a]	Barnaul	Chebula	Krasnozerskoye	Salair East	Salair West	Tomsk
Ecological zone	Forest-steppe (southern part)	Forest-steppe (northern part)	Steppe to Forest-steppe	Sub-taiga to Forest-steppe	"Blackish taiga"	Sub-taiga
Latitude (°N)	53.41	55.55	53.59	54.39	54.18	56.30
Longitude (°E)	83.47	84.00	79.14	85.75	85.17	85.43
Elevation (m asl)	221	186	141	305	358	232
Climate characteristics (annual mean 1981–2010)						
Air temperature (°C)	2.7	1.3	2.9	2.3	1.2	0.9
Precipitation (mm)	431.5	509.8	324.5	432.3	453.0	566.5
Soil classification						
Soil in forest	Haplic Phaeozem	Haplic Phaeozem	Phaeozem	Leptic Phaeozem	Haplic Luvisol	Albic Luvisol
Soil in grassland	Calcic Chernozem	Haplic Phaeozem	Calcic Hortic Chernozem	Leptic Phaeozem		Albic Luvisol
Forest stand characteristics (mean values)						
Density (tree ha^{-1})	1664	387	767	1883	1144	1139
DBH[b] (cm)	14.9	33.9	26.3	13.7	22.8	21.4
Height (m)	11.2	28.0	18.7	15.7	24.8	18.2
Age (years)	27	62	51	21	47	56

[a]name of the closest city or name of the local area; [b]diameter at breast height (1.3 m)

6.2 Materials and methods

6.2.1 Site description

Many soils of south-western (SW) Siberia have developed on loess deposits—the Eurasian loess belt covers a broad latitudinal zone between 40 and 60 ° N—and present a favourable texture and mineralogy for plant growth (Chlachula 2003; Muhs 2007). Soil formation depends on climatic conditions, vegetation cover and can be further shaped by anthropogenic actions. All of these—climatic conditions, vegetation cover and human activities—differ in intensity essentially along a gradient from south to north. Consequently, from the common origin of loess deposits, the soils in SW Siberia have undergone different types of development and are classified as belonging to the main groups of Chernozems, Phaeozems and Luvisols. Water-table movements, the leaching of carbonates and organic matter accumulation or organic matter distribution throughout the profile are the most striking features in these soils. The soil-forming processes related to soil moisture levels and dynamics as well as the stability of organic matter (mineralization rates in relation to temperature and moisture regimes) and the type of vegetation are known to influence the soil P status (Giesler et al. 2002; Miller et al. 2001; Sundqvist et al. 2014; Vincent et al. 2014). We selected six sites in SW Siberia covering a transition including forest-steppe and sub-taiga zones. The main site characteristics are given in Table 6.1 (see also Tables D.1 to D.3 and Brédoire et al. 2016b, Chap. 5).

All the soil profiles studied had developed on a loess parent material and vegetation cover had comparable features in terms of dominant species composition, stand age and low human impact (i.e. no active management for the last few decades; Tables D.2 and D.3). The main characteristics of the initial loess material are the predominance of coarse-silt particles and clay and the presence of $CaCO_3$, the latter having had different fates related to the different soil development processes. At Barnaul (BAR), Chebula (CHE), Krasnozerskoye (KRA) and Salair East (SAE), the main soil-forming processes are the formation and accumulation of organic matter, leaching of carbonates in the topsoil and formation of secondary carbonates in deep soil layers. Soils belong to the Chernozems and Phaeozems soil groups. In Salair West (SAW) and Tomsk (TOM), soils experience water-table movements, with periodical saturation. Consequently, clays are washed from the topsoil and accumulate in the deeper layers and carbonates have disappeared from the first metre of the soil profile. In addition, the litter decomposes faster than in forest-steppe and the accumulation of organic matter is very low at the soil surface. At these two sites, soils belong to the Luvisols group.

Five of the sites were almost pure aspen (*Populus tremula* L.; Table D.2) forest stands together with nearby grassland areas. Only one site (SAW) had forest cover with aspen. So there were six forest sites and five with grassland in our data set for

SW Siberia. All aspen stands had closed canopies.

6.2.2 Sampling and preparation of the samples

For each type of vegetation cover at each site, we delimited three study plots (about 300 m^2) about 200–2000 m apart. Those three plots were considered replicates. One sampling campaign permitted sampling at all sites within 3 weeks in July 2013. At each plot, we dug a soil pit (with a surface area of about 2 × 1 m) down to 120 cm, except at SAE grasslands where we reached a dense schist material at around 80 cm which prevented us from going any deeper than 100 cm. In each soil pit, about 1 kg of soil was sampled horizontally with hand tools at depths of 5, 15, 30, 60 and 100 cm ± 5 cm. Another sample was taken with a cylinder (97 cm^3) to assess soil density.

Litter was sampled over an area of 30 cm by 40 cm in the vicinity of each soil pit. In this study we defined all the dead plant material deposited on the soil surface as "litter" (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands). Consequently, the material collected in July, 2013 resulted mostly from the dead material from the previous vegetation season (2012) and the residues of older seasons, that is to say mainly OL and OF horizons, and possibly OH (at BAR, CHE, KRA and SAE).

Bulk soil samples were air-dried to a constant weight. After drying, soil samples from the same site and the same vegetation cover (i.e. three samples per site and per vegetation cover) were pooled and sieved at 2 mm to remove stones and coarse roots. Such soil preparation was reported to affect biogeochemical processes only at a low magnitude (Černohlávková et al. 2009; Chapman et al. 1997). Soil density samples were not pooled. They were oven dried at 105 °C for 48 h and stones were removed when present (i.e. only in deep horizons of SAE).

Bulk litter samples were oven dried at 60 °C to a constant weight. They were then pooled by site and by vegetation cover and the composite samples (three per site and per vegetation cover) were ground before chemical analyses except for the isotopic dilution.

6.2.3 Physico-chemical analyses

Main soil properties

The French standard methods (Association Française de NORmalisation; AFNOR 1999) were used for most of the physico-chemical soil analyses. For soil texture, the five size fractions for clay (<2 µm diameter), fine loam (2–20 µm), coarse loam (20–50 µm), fine sand (50–200 µm) and coarse sand (200–2000 µm) were assessed after decarbonation (NF X 31–107). Soil pH–H_2O was determined in a water–soil suspension with a mass-to-volume ratio of 1 g: 2.5 mL (NF ISO 10390). Total organic

C and N contents were determined by dry combustion with oxygen (NF ISO 10694 and NF ISO 13878, respectively). Total calcium carbonate contents were assessed using a volumetric method (NF X 31–105). Poorly crystalline aluminium (Al) and iron (Fe) oxides were extracted with an ammonium oxalate solution (McKeague and Day 1966).

Total, organic and inorganic P

Total P concentrations (P_{tot}, in $\mu g\, g^{-1}$ soil) were determined, after grinding, by ICP following wet digestion with concentrated fluoric (HF) and perchloric acids after calcination at 450 °C based on a normalized procedure (AFNOR NF X 31–147; AFNOR 1999). Total soil organic P concentrations (P_{org}, in $\mu g\, g^{-1}$ soil) were determined as the difference between P extracted with H_2SO_4 in ignited and non-ignited soil samples (2 g of dry soil for 70 mL of 0.2 N H_2SO_4; Saunders and Williams 1955); concentrations were determined with a green malachite colorimetric method (van Veldhoven and Mannaerts 1987). Total inorganic P concentrations (P_{inorg}, in $\mu g\, g^{-1}$ soil) were subsequently calculated as the difference between P_{tot} and P_{org}.

Plant-available phosphate ions

Plants take up P as ions from the soil solution. Thus, a good way of estimating a realistic plant-available P pool in the soil is to quantify both the concentration of phosphate ions in solution and the capacity of the solid phase to maintain this concentration.

To do this, we quantified the phosphate ions in the soil solution (Cp in $\mu g\, mL^{-1}$ soil solution or Qw in $\mu g\, g^{-1}$ soil) and the diffusive phosphate ions at the solid–solution interface (Pr in $\mu g\, g^{-1}$ soil). Pr is the quantity of phosphate ions that can be exchanged between solid constituents (ions are adsorbed on soil particles) on a concentration gradient. Pr results from molecular agitation; it can be considered as a "P buffering capacity". The sum of Pr and Qw is the isotopically exchangeable phosphate ions (E), and it is considered a good proxy for the gross amount of plant-available P (Fardeau 1996; Morel and Plenchette 1994). Cp and Pr were determined by an isotopic dilution kinetics method (Fardeau 1996; Frossard and Sinaj 1997; Frossard et al. 2011) as described below.

For each litter or mineral soil sample, five suspensions (1 g of litter or soil with 10 mL of deionized water) were equilibrated for 16 h on a roller (40 cycles min^{-1}) at 20 °C (this temperature is commonly reported in the literature and is close to the average temperature of the soil at 20 cm in our study sites in the summer; Table D.1). Toluene (0.1 mL; M. Lineres, unpublished results) was added to the suspension at the beginning in order to stop microbial activity. This biocide does not affect P biochemical processes (Bünemann et al. 2007). The phosphate ions in solution of

the pre-equilibrated suspensions were labelled by introducing carrier-free ^{32}P ions in negligible concentrations but with known amounts of introduced radioactivity (R). Suspensions were then sampled with a plastic syringe after 4, 10, 40, 100 and 400 min and filtered on a membrane at 0.2 µm. Then, both the Cp and radioactivity remaining in the filtered solution at the time of sampling ($r(t)$) were quantified. Cp was determined using a green malachite colorimetric method (van Veldhoven and Mannaerts 1987) and Qw was calculated using the volume of water (V in mL) and the mass of litter or soil (m_s in g):

$$Qw = Cp \times \frac{V}{m_s} \tag{6.1}$$

For each sample, Cp was not impacted by the sampling time of the isotopic dilution method (Fig. D.1). The radioactivity remaining in the filtered solution ($r(t)$) was determined in a counter (Packard TR 1100) using a liquid scintillation cocktail. In the steady-state conditions of the suspension (Cp constant), the gross transfer of phosphate ions from the solid constituents to the solution is equal to the gross transfer of phosphate ions from the solution onto the solid constituents. We assumed that no isotopic discrimination occurs between the two P isotopes (^{31}P ions and ^{32}P ions) during the transfers between the liquid and the solid phases. The amount of unlabelled phosphate ions newly transferred from the solid constituents to the solution ($Pr(t)$) was then calculated from Qw and $r(t)$ values following the principle of isotopic dilution (R is diluted in E).

$$\frac{R}{E} = \frac{r(t)}{Qw} = \frac{R - r(t)}{Pr(t)} \tag{6.2}$$

Rearranging Eq. 6.2 gives:

$$Pr(t) = \frac{Qw \times (R - r(t))}{r(t)} = Qw \left(\frac{1}{r(t)/R} - 1 \right) \tag{6.3}$$

where $\frac{r(t)}{R}$ (dimensionless) is the isotopic dilution ratio.

The theoretical Eq. 6.4, adapted from Fardeau (1993, 1996) was used to fit the experimental values of $\frac{r(t)}{R}$ closely, as a function of isotopic dilution time:

$$\frac{r(t)}{R} = m(t + m^{\frac{1}{n}})^{-n} \text{ for } \frac{r(t)}{R} \geqslant \frac{r(\infty)}{R} \tag{6.4}$$

where m and n are fitting parameters and $\frac{r(\infty)}{R}$ corresponds to the maximum possible dilution of the isotope considering that all inorganic P can take part in the isotopic dilution. The value of $\frac{r(\infty)}{R}$ tends towards $\frac{Qw}{P_{inorg}}$ (Fardeau 1993; Frossard et al. 2011). The parameter m, which is the fraction of radioactivity remaining in solution after

1 min ($\frac{r(1min)}{R}$), accounts for the immediate physico-chemical reactions while the parameter n accounts for the slow ones (Fardeau 1993; Fardeau et al. 1991). The quality of the fit for Eq. 6.4 is shown in Fig. D.2, and the values of m and n are provided in Table D.5.

Combining Eq. 6.3 and Eq. 6.4, we can derive the value of Pr over time, each value corresponding to a pool of P more or less rapidly available to plants. The number and the size of such pools can be defined considering plant functioning (Fardeau 1993). In this study, we computed the values of Pr for 1 day, 1 week and 3 months. While 1 day is the mean duration for active root uptake, 3 months is approximately the duration of the vegetation season in south-western Siberia and we might expect this to fit with intense root activity.

6.2.4 Data handling and statistics

Five soil layers were defined between 0 and 120 cm according to the soil horizon description of each soil pit (horizons were merged or divided in order to have five layers corresponding to the five sample depths, the profiles studied presented between four and seven horizons, the mean number of horizons of the 33 profiles studied is five). Assuming that elemental concentrations and soil densities measured in each of the five defined horizons were representative of the entire horizon, we computed the stock (in Mg ha^{-1}) of each P pool using mean soil densities and horizon thicknesses:

$$stock = \frac{1}{10000} \times [P] \times d \times h \tag{6.5}$$

where $[P]$ is the concentration of the P pool (in µg g^{-1}), d the soil density (in g cm^3) and h the thickness of the soil horizon in cm. In litter, the P stocks were computed (in Mg ha^{-1}) using the mass and the surface area sampled:

$$stock = \frac{1}{10000} \times [P] \times m_{litter} \tag{6.6}$$

where $[P]$ is the concentration of the P pool (in µg g^{-1}) and m_{litter} the mass of litter (in g m^{-2}). We used the limit of −20 cm to distinguish between top- and subsoil to fit with most agronomic studies but also with the zone where most of the fine-root exploration occurs in SW Siberia (Brédoire et al. 2016b, Chap. 5).

In order to gain an idea of the structure of the P stocks in the soils studied, we computed the relative proportions of the different P pools measured as a fraction of P_{tot}. P_{tot} is the sum of P_{org} and P_{inorg}. Since a biocide was added to the suspension, mineralization was stopped and we only measured physico-chemical processes. Thus, all exchangeable P (the sum of Qw and Pr) is part of P_{inorg}. Pr being calculated as a function of time and the maximum time considered in this study being 3 months, the potential remaining fraction of P_{inorg} is considered as non-diffusive, or diffusive

in more than 3 months. We note that when considering two values of *Pr* computed at different times, the pool of exchangeable P computed at the longer time includes the one computed at a shorter time.

Relations between P parameters and soil physico-chemical properties were investigated by computing Spearman's rank correlation coefficients, scatter plots and (non-)linear regressions. Soil physico-chemical properties varied with soil depth (Table D.4) as well as the P parameters investigated (Table 6.2). Thus, we looked for correlations in each soil layer separately in order to avoid covariation and interdependence issues (Table D.6). We also analysed correlations with fine-root (diameter < 0.8 mm) length density (FRLD) and fine-root mass density (FRMD) measured in the same soil pits and at the same soil depths as for the soil physico-chemical properties (Brédoire et al. 2016b, Chap. 5).

Since analyses were made on composite samples, we did not quantify the variability of our measurements at the site level for a given vegetation cover and soil depth. Thus, differences between sites were not tested through formal statistical tests. However, we calculated the coefficient of variation (ratio of the standard deviation to the mean) for each layer and vegetation cover.

All data management, (non-)linear regressions and statistical analyses (correlation coefficients and their significance), were performed with R 3.2.1 (R Core Team 2015).

6.2.5 Comparison on the global scale

To compare the phosphorus status of our study sites with other grassland or forest ecosystems and with croplands, we compiled data on different P fractions in soils. In practice, we used different requests involving keywords such as "soil", "phosph*", "total content", "isotopic dilution", "isotopically exchangeable P", "grassland", "forest", "woodland", etc. These requests were carried out both in Web of Science and Google Scholar. To derive the pools of diffusive and isotopically exchangeable phosphate ions, we selected all publications using the same isotopic dilution procedures as in the present study (i.e. Fardeau's procedure; Fardeau 1993, 1996). Additional publications were selected in order to improve the geographical coverage for total and organic P. In particular, we examined all the tables of contents of the *Soviet Soil Science* and the *Eurasian Soil Science* journals to provide a better cover of Northern Eurasian ecosystems. Based on all the selected references, we compiled a data set of different P fractions (total P, organic P, phosphate ions in soil solution, diffusive phosphate ions and isotopically exchangeable phosphate ions) in soils of grasslands, forests and croplands. This data base contained P values for up to 373 distinct sites depending on the P fraction, the geographical scale and the vegetation type studied, which were collected from 236 references. This data base was representative of soils throughout the world as shown by the geographical distribution of compiled sites (Fig. 6.1), even though the studies using the isotopic dilution kinetics method in forest were sparse.

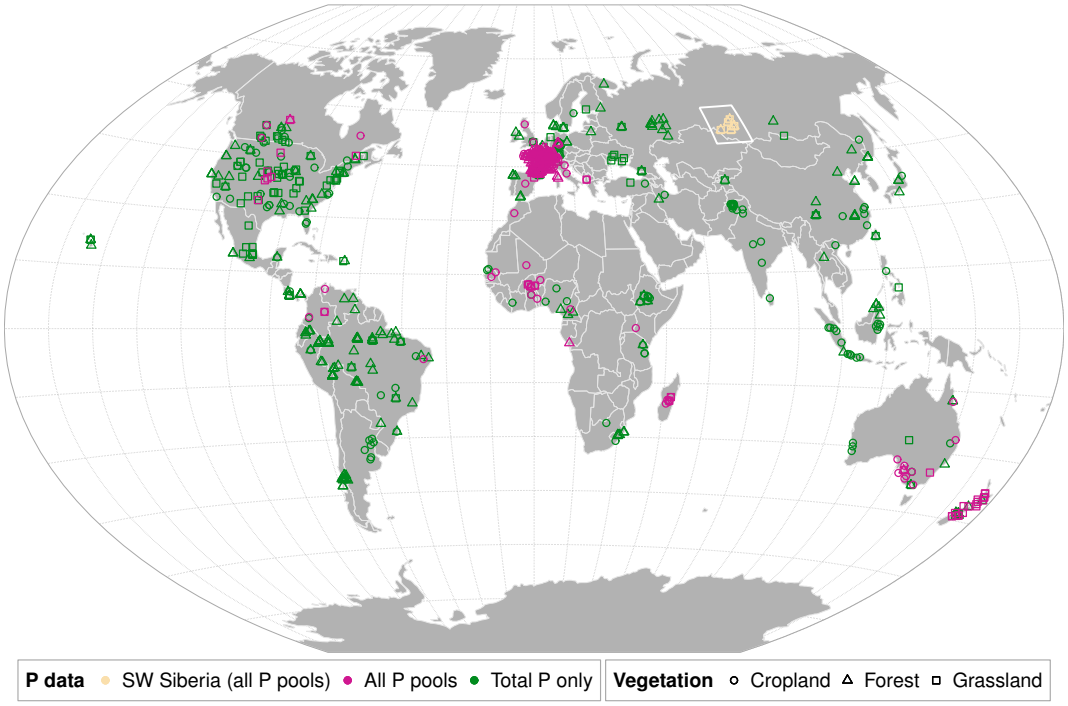


Figure 6.1: Location of the study sites (south-western Siberia outlined by the white box, data points are beige) and the data points from a literature compilation. Distinction is made between the quantity of information available for each point (colour) and between vegetation cover (shape). "All P pools" stands for total P, organic P, inorganic P, phosphate ions in soil solution, diffusive phosphate ions and isotopically exchangeable phosphate ions. Winkel tripel projection; graticules 15°.

Out of the 116 forest study sites present in the compilation—with values for inorganic P, organic P, phosphate ions in solution, diffusive phosphate ions and isotopically exchangeable phosphate ions—, 106 are located in France. Nevertheless, France does have very diverse soils and geology. The most represented soil types are Podzols, Cambisols and Luvisols, but Planosols, Leptosols, Calcisols, Arenosols, Regosols and Andosols are also present at some sites (IUSS Working Group WRB 2014). The main parent materials are calcareous formations, eruptive and metamorphic rocks, sandstone, and detritic and weathered formations. Of these 106 French sites, 50 are hardwood forests (two species) and 56 are coniferous forests (five species). Therefore, our data set was representative of forests on the global scale for total soil P, and representative of very diverse temperate forests for isotopic P data. The references of the data compilation are provided in the Appendix D.

6.3 Results

6.3.1 Quantification of P pools

The concentrations of total P (P_{tot}; 694–1095 µg g^{-1} at −5 cm, 319–694 µg g^{-1} at −100 cm), organic P (P_{org}; 389–774 µg g^{-1} at −5 cm, 37–79 µg g^{-1} at −100 cm) and phosphate ions in solution (Qw; 2–22 µg g^{-1} at −5 cm, 0.1–0.4 µg g^{-1} at −100 cm) decreased with depth in the 1 m profiles at all the sites studied for both forest and grassland (Table 6.2). The litter layer presented the highest concentrations for these pools, Qw being 1 to 2 order(s) of magnitude more concentrated in the litter (223–638 µg g^{-1}) than in the upper soil layer (2–22 µg g^{-1} at −5 cm). No systematic variation with depth was found throughout the profile for inorganic P (P_{inorg}; 296–626 µg g^{-1} at −5 cm, 282–616 µg g^{-1} at −100 cm) and diffusive phosphate ions (e.g. Pr (1 day); 16–56 µg g^{-1} at −5 cm, 2–67 µg g^{-1} at −100 cm; Table 6.2). However, Pr (1 day) decreased in the three first mineral soil layers except for the grassland at SAE.

We computed stocks (Mg ha^{-1}) for the different P pools (Table 6.3). With the exception of Qw, the subsoil contributed the most to the total stocks (72–85 % of P_{tot}, 64–73 % of P_{org} excluding SAE, 82–90 % of P_{inorg} and 67–94 % of Pr (1 day)). The three layers considered (litter, topsoil and subsoil) contributed almost equally to the total stock of Qw (respectively, 10–56 %, 26–65 % and 7–49 %). All sites presented values of the same order of magnitude for a given P pool and a given layer. The values for forest and grassland were also close. One notable difference occurred at the site SAE, where soil P pools were lower in forest than in grassland and where the pools in forest were lower than in the other sites. KRA presented the highest stocks in litter for all P pools, however, its stocks in the topsoil were the lowest (except for Qw and Pr (1 day) in grassland) and they were also relatively low in the subsoil.

For each layer, we calculated the relative contribution of each P pool to total P (Fig. 6.2). With the exception of one grassland site (TOM), P_{org} accounted for more than 50 % of P_{tot} in the litter layer. The concentration of phosphate ions in solution (Qw) represented 20–38 % of P_{tot} in the litter layer with similar values for forest and grassland at each site. One site (TOM) presented much higher values of Qw in litter, reaching 45 and 67 % of P_{tot} in forest and grassland respectively. All the sites studied, whatever the vegetation cover, exhibited the same pattern along the mineral soil profile. The relative proportion of P_{org} decreased while the relative proportion of P_{inorg} increased with depth. In the two upper soil layers the distribution of P pools was very comparable. P_{org} accounted for 34–71 % of P_{tot} and Pr (3 months) for 3–13 %. Qw represented up to 2 % of P_{tot} at −5 cm, dropped below 0.1 % at −30 cm and was about 0.01 % at −100 cm. The proportions of Pr tended to be higher in forest than in grassland. Below −15 cm, the proportion of P_{org} decreased to 6–19 % at −100 cm. In the deepest layers, the proportions of Pr tended to be higher than in the first two,

Table 6.2: Phosphorus concentrations of different pools measured in litter and soil layers of south-western Siberia. Concentrations are expressed in $\mu g\,P\,g^{-1}$ soil (or litter); depth is in cm. "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands), i.e. mainly OL and OF horizons and possibly OH (at BAR, CHE, KRA and SAE) at the date of sampling.

	Depth	Forest							Grassland					
P pool	(cm)	BAR	CHE	KRA	SAE	SAW	TOM	*CV*	BAR	CHE	KRA	SAE	TOM	*CV*
Total P	Litter	1235.6	1174.5	1318.6	1231.3	1515.1	1011.8	*13*	1165.8	1340.4	1122.1	1318.6	953.1	*13*
	−5	1017.3	851.4	729.2	1095.9	1039.2	759.7	*17*	877.6	956.2	847.0	921.3	694.2	*12*
	−15	951.8	663.7	615.6	908.2	864.5	676.8	*19*	864.5	938.7	698.6	873.2	624.4	*17*
	−30	960.6	628.7	541.4	416.1	768.5	558.9	*30*	755.4	899.4	628.7	563.2	528.3	*23*
	−60	764.1	676.8	394.7	323.5	585.1	489.0	*31*	593.8	689.9	515.2	611.3	493.4	*14*
	−100	637.5	659.3	408.2	319.2	646.2	528.3	*27*	593.8	694.2	414.4	593.8	537.0	*18*
Organic P	Litter	817.3	760.1	839.5	896.2	910.8	758.9	*8*	800.5	690.4	640.7	855.5	660.0	*13*
	−5	391.6	405.6	418.5	773.7	470.0	436.1	*30*	388.8	539.2	539.5	521.8	398.7	*16*
	−15	319.6	286.8	335.1	614.6	379.4	375.7	*31*	358.3	472.2	413.7	495.6	333.6	*17*
	−30	332.1	208.7	286.4	202.6	284.3	217.5	*21*	276.9	422.0	343.6	100.3	206.1	*46*
	−60	156.8	133.5	96.9	58.2	114.7	137.8	*30*	108.1	90.1	201.4	123.4	89.7	*38*
	−100	50.3	58.8	79.5	37.1	68.5	63.5	*25*	48.6	78.7	45.7	37.0	64.5	*30*
Inorganic P	Litter	418.3	414.4	479.1	335.1	604.3	253.0	*29*	365.3	650.0	481.4	463.1	293.1	*30*
	−5	625.7	445.8	310.7	322.2	569.2	323.7	*32*	488.8	417.0	307.6	399.4	295.5	*21*
	−15	632.2	376.9	280.5	293.6	485.1	301.1	*35*	506.3	466.5	284.9	377.7	290.8	*26*
	−30	628.5	420.1	255.1	213.5	484.2	341.4	*39*	478.5	477.4	285.2	462.9	322.2	*23*
	−60	607.3	543.3	297.8	265.3	470.4	351.2	*33*	485.7	599.7	313.9	487.9	403.7	*23*
	−100	587.1	600.5	328.8	282.1	577.7	464.8	*29*	545.2	615.5	368.7	556.8	472.6	*19*

CV: coefficient of variation (ratio of the standard deviation to the mean, in %).

Table 6.2: Continued.

		Forest							Grassland					
P pool	Depth (cm)	BAR	CHE	KRA	SAE	SAW	TOM	*CV*	BAR	CHE	KRA	SAE	TOM	*CV*
Phosphate	Litter	353.2	397.6	406.1	343.8	500.4	457.1	*15*	393.7	520.7	223.2	271.2	637.8	*42*
ions in	−5	10.3	15.8	11.2	22.1	17.9	1.5	*55*	6.4	2.9	13.7	1.9	1.7	*95*
soil	−15	5.3	2.3	1.5	6.0	3.3	1.6	*57*	1.0	1.3	1.1	1.0	0.7	*23*
solution	−30	3.6	0.8	0.7	0.4	0.9	0.2	*114*	0.4	0.8	0.8	0.5	0.1	*56*
	−60	1.1	0.3	0.5	0.1	0.2	0.2	*89*	0.2	0.3	0.7	0.7	0.2	*62*
	−100	0.2	0.2	0.2	0.1	0.4	0.3	*44*	0.2	0.2	0.4	0.1	0.1	*50*
Diffusive	Litter	88.8	84.2	72.9	80.0	103.9	37.3	*29*	36.6	23.5	59.9	85.8	3.0	*77*
phosphate	−5	42.5	56.1	34.9	53.4	48.1	26.3	*26*	31.6	20.3	36.1	21.1	16.2	*33*
ions in	−15	33.1	25.0	17.1	26.7	35.4	26.2	*24*	21.5	15.8	27.3	22.8	18.7	*20*
1 day	−30	29.2	15.3	26.6	15.6	24.6	11.9	*35*	16.6	13.5	17.7	40.8	13.7	*56*
	−60	39.6	38.4	30.5	14.7	25.4	29.9	*31*	20.0	48.5	20.4	13.4	89.4	*82*
	−100	24.3	40.4	32.3	2.2	66.7	57.4	*62*	17.5	35.3	47.4	2.5	36.3	*64*
Diffusive	Litter	88.8	84.2	72.9	80.0	103.9	37.3	*29*	36.6	23.7	74.3	109.8	3.0	*86*
phosphate	−5	64.7	92.7	52.0	79.8	74.5	57.3	*22*	47.8	33.1	53.8	33.7	29.4	*27*
ions in	−15	52.9	45.9	29.8	43.5	70.0	51.0	*27*	34.2	26.8	51.3	42.7	39.3	*24*
1 week	−30	46.4	28.8	57.2	29.4	51.5	26.6	*33*	28.4	24.3	30.9	71.0	31.7	*51*
	−60	70.1	73.9	51.1	31.9	53.9	64.4	*27*	35.2	95.9	37.1	20.2	178.7	*89*
	−100	47.0	73.1	61.7	4.0	137.6	91.8	*65*	30.4	65.1	94.3	4.6	64.5	*67*
Diffusive	Litter	88.8	84.2	72.9	80.0	103.9	37.3	*29*	36.6	24.0	94.3	143.7	3.0	*96*
phosphate	−5	108.7	170.4	84.5	129.2	125.8	155.5	*24*	80.1	61.0	87.1	61.6	62.4	*17*
ions in	−15	95.3	99.1	60.4	79.1	166.4	119.5	*36*	62.4	52.4	116.4	96.2	102.6	*32*
3 months	−30	83.4	65.0	154.6	66.7	133.8	75.6	*39*	57.1	51.5	63.5	146.2	94.5	*48*
	−60	147.4	174.1	100.3	87.9	144.2	175.4	*27*	73.9	234.2	80.4	34.1	403.4	*93*
	−100	111.5	159.3	144.1	8.5	355.3	169.6	*71*	62.4	145.0	231.7	10.2	136.9	*72*

CV: coefficient of variation (ratio of the standard deviation to the mean, in %).

Table 6.3: Stocks of the different P pools computed in Mg ha^{-1} for the litter, the topsoil (about 0 to −20 cm), the subsoil (about −20 to −120 cm) and for the whole profile for the different sites. "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands), i.e. mainly OL and OF horizons and possibly OH (at BAR, CHE, KRA and SAE) at the date of sampling.

		Forest							Grassland					
P pool	Layer	BAR	CHE	KRA	SAE	SAW	TOM	*CV*	BAR	CHE	KRA	SAE	TOM	*CV*
Total P	Litter	0.037	0.028	0.057	0.024	0.014	0.012	*58*	0.008	0.003	0.026	0.012	0.002	*95*
	Topsoil	2.549	1.749	1.121	1.462	1.729	1.433	*29*	2.338	2.030	1.464	2.089	1.432	*22*
	Subsoil	9.728	8.865	6.247	3.887	10.190	7.287	*31*	9.541	9.682	6.848	7.740	7.366	*16*
	Total	**12.313**	**10.642**	**7.424**	**5.374**	**11.934**	**8.732**	***29***	**11.888**	**11.714**	**8.338**	**9.840**	**8.800**	***16***
Organic P	Litter	0.024	0.018	0.036	0.018	0.009	0.009	*55*	0.006	0.001	0.015	0.008	0.001	*89*
	Topsoil	0.894	0.782	0.622	1.003	0.764	0.805	*16*	0.995	1.079	0.896	1.185	0.791	*16*
	Subsoil	2.010	1.520	1.787	0.958	2.075	1.705	*24*	1.809	2.002	1.964	1.043	1.604	*23*
	Total	**2.928**	**2.320**	**2.445**	**1.978**	**2.848**	**2.518**	***14***	**2.809**	**3.082**	**2.875**	**2.235**	**2.396**	***13***
Inorganic P	Litter	0.012	0.010	0.021	0.007	0.006	0.003	*65*	0.003	0.001	0.011	0.004	0.001	*107*
	Topsoil	1.655	0.967	0.498	0.459	0.965	0.628	*52*	1.344	0.951	0.568	0.904	0.641	*35*
	Subsoil	7.718	7.345	4.460	2.929	8.116	5.582	*34*	7.732	7.680	4.883	6.696	5.762	*19*
	Total	**9.385**	**8.322**	**4.979**	**3.395**	**9.086**	**6.214**	***35***	**9.078**	**8.631**	**5.462**	**7.605**	**6.404**	***20***
Phosphate	Litter	0.010	0.010	0.017	0.007	0.005	0.005	*52*	0.003	0.001	0.005	0.002	0.001	*63*
ions in	Topsoil	0.018	0.015	0.008	0.016	0.012	0.003	*45*	0.008	0.004	0.012	0.003	0.002	*67*
soil	Subsoil	0.017	0.004	0.006	0.002	0.008	0.003	*83*	0.003	0.005	0.008	0.005	0.002	*44*
solution	**Total**	**0.045**	**0.029**	**0.031**	**0.024**	**0.025**	**0.012**	***40***	**0.014**	**0.010**	**0.025**	**0.011**	**0.006**	***54***

CV: coefficient of variation (ratio of the standard deviation to the mean, in %).

Table 6.3: Continued.

		Forest							Grassland					
P pool	Layer	BAR	CHE	KRA	SAE	SAW	TOM	*CV*	BAR	CHE	KRA	SAE	TOM	*CV*
Diffusive	Litter	0.003	0.002	0.003	0.002	0.001	0.000	*56*	0.000	0.000	0.001	0.001	0.000	*118*
phosphate ions	Topsoil	0.094	0.083	0.039	0.052	0.073	0.054	*32*	0.068	0.038	0.059	0.052	0.039	*25*
in 1 day	Subsoil	0.397	0.480	0.447	0.110	0.741	0.532	*45*	0.280	0.464	0.496	0.187	0.588	*41*
	Total	**0.494**	**0.565**	**0.490**	**0.164**	**0.815**	**0.586**	***41***	**0.348**	**0.503**	**0.557**	**0.240**	**0.627**	***35***
Diffusive	Litter	0.003	0.002	0.003	0.002	0.001	0.000	*56*	0.000	0.000	0.002	0.001	0.000	*122*
phosphate ions	Topsoil	0.148	0.144	0.064	0.081	0.136	0.108	*31*	0.106	0.064	0.101	0.093	0.077	*20*
in 1 week	Subsoil	0.707	0.898	0.843	0.223	1.535	0.937	*49*	0.487	0.882	0.961	0.313	1.142	*46*
	Total	**0.858**	**1.044**	**0.910**	**0.306**	**1.673**	**1.045**	***45***	**0.593**	**0.945**	**1.064**	**0.407**	**1.219**	***40***
Diffusive	Litter	0.003	0.002	0.003	0.002	0.001	0.000	*56*	0.000	0.000	0.002	0.001	0.000	*126*
phosphate ions	Topsoil	0.260	0.291	0.117	0.141	0.304	0.267	*35*	0.186	0.121	0.202	0.199	0.187	*19*
in 3 months	Subsoil	1.506	2.037	1.951	0.563	3.979	2.032	*56*	1.005	2.045	2.286	0.616	2.623	*50*
	Total	**1.769**	**2.330**	**2.071**	**0.705**	**4.284**	**2.300**	***52***	**1.191**	**2.166**	**2.491**	**0.816**	**2.810**	***45***

CV: coefficient of variation (ratio of the standard deviation to the mean, in %).

with notable exceptions: extremely low values at −100 cm at SAE, and *Pr* (3 months) representing 100 % of P_{inorg} at −60 cm at TOM grassland.

6.3.2 Relations between P pools and environmental parameters

We tested the correlations between P parameters and the main soil physico-chemical properties (Table D.6 and Fig. D.3). P_{inorg} was significantly correlated with P_{tot} (Spearman's rank correlation coefficients ranging between 0.627 and 0.989). This was also observed between *n* and pH at most depths except at −15 and −100 cm (−0.636 to −0.793). In the three top layers, P_{org} was significantly correlated with organic C (0.682 to 0.843) and *m* with *Qw* (0.609 to 0.855). In the two deepest layers, *Pr* and isotopically exchangeable phosphate ions (*E*) were significantly correlated with the clay fraction (0.782 and 0.852). They were also negatively correlated with $CaCO_3$ (−0.649) at −60 cm (Table D.6) but this was driven by one point which was very depleted in $CaCO_3$ and with very high *Pr* and *E* (Fig. D.3). A few correlations were found with Al and Fe oxides: with P_{org} at −30 cm (−0.636) and with *n* at −60 cm (0.718).

A few relationships between fine-root densities and P pools were significant (Table D.6 and Fig. D.3). At −15 cm, fine-root length density (FRLD) was significantly and negatively correlated with *Qw* (−0.636), *m* (−0.764), *Pr* (1 day) (−0.691) and *E* (1 day) (−0.736). At −30 cm, FRLD was significantly and negatively correlated with *n* (−0.773) and fine-root mass density (FRMD) with *n* (−0.655), *Pr* (0.636) and *E* (0.618).

No relationship was found between the different variables of the P status and any of the climatic parameters presented in Table D.1 (data not shown).

6.3.3 Comparison on the global scale

Total P concentrations in topsoil (the first 20 cm of the soil) ranged on the global scale between 62 and 2480 µg g^{-1} in croplands, between 19 and 3090 µg g^{-1} in forests and between 32 and 3548 µg g^{-1} in grasslands (Fig. 6.3). Our measurements in SW Siberia ranged between 345 and 770 µg g^{-1} in forests and between 481 and 741 µg g^{-1} in grasslands, these values were close to and above the global upper quartile for forests and between the global median and the upper quartile for grasslands. Compared with global cropland values these Siberian concentrations were mostly above the upper quartile. Restricting the domain of comparison to Northern Eurasia, SW Siberian soils ranged between the lower and the upper quartiles for forests and between the median and the upper quartile for grasslands, indicating that our sites are representative of Northern Eurasia. In the subsoil (−20 to −100 cm), less points were available at the global and on Northern Eurasian scales for comparison. However,

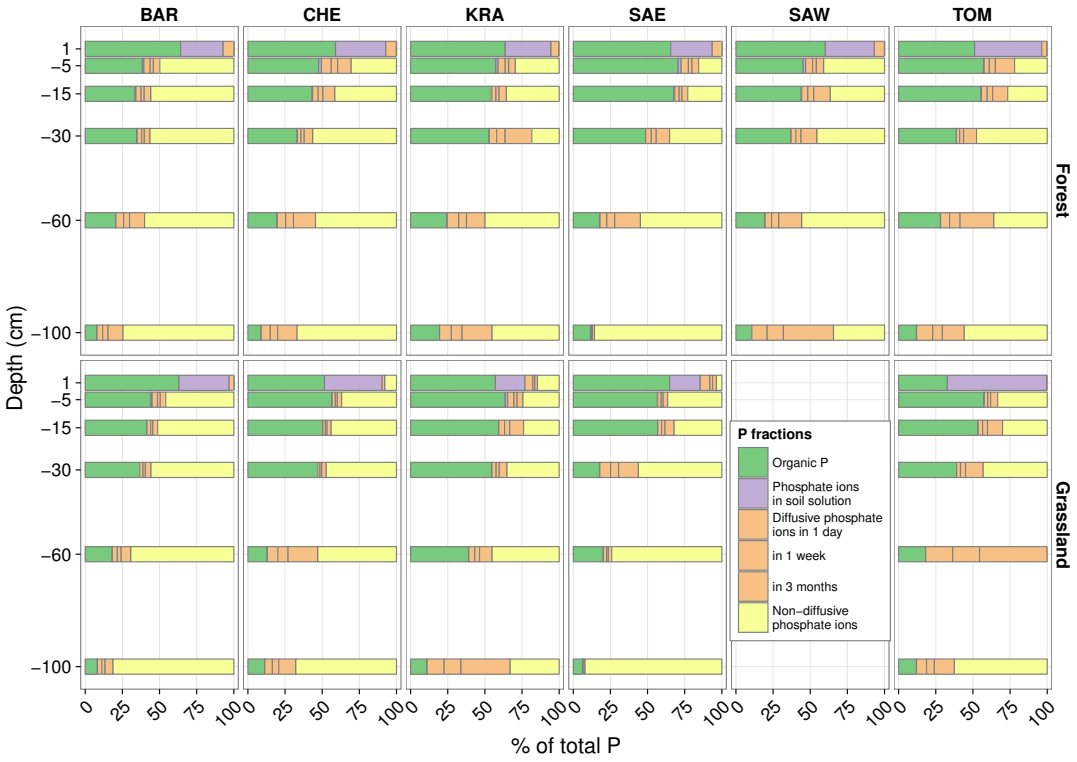


Figure 6.2: Structure of total P (P_{tot}) in terms of P ions in the soil solution (Qw), diffusive P ions on different timescales (Pr), and non-diffusive P ions or those that are diffusive in more than 3 months ($P_{non-diff}$). Each fraction of P is expressed as percentage of P_{tot}. Note that the diffusive fractions for the shorter times are included in the diffusive fraction for the longer time (e.g. Pr(1 day) is included in Pr(1 week) and they are both included in Pr(3 months)). Depth "1" is the litter. "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands) i.e. mainly OL and OF horizons, and possibly OH (at BAR, CHE, KRA and SAE) at the date of sampling.

our SW Siberian forest and grassland soils occupied wider ranges in comparison to the corresponding vegetation types: from below the median to above the upper quartile on the global scale, with a similar range of values to Northern Eurasia.

The concentrations of P_{org}, P_{inorg} and phosphate ions in solution (Cp) in the topsoil of the SW Siberian forests studied were generally above the upper quartile, in comparison essentially with French forests having contrasting species, soil and geology (Fig. 6.4). In grassland, the SW Siberian values were mostly located between the global median and upper quartile. Compared with global cropland ranges, our measurements were around and above the upper quartile for P_{tot} and P_{org}, mainly below the upper quartile for P_{inorg} and from the median to above the upper quartile for Cp. Interestingly, the proportion of measured P_{org} (% of P_{tot}) varied quite a lot in the range reported on the comparative scales, particularly in forests where SW Siberian values varied from below the lower quartile to above the upper quartile. In contrast with the other P pools, the concentrations of Pr (1 day) and E (1 day) were more moderate: they ranged between the median and the upper quartile in forests and between the lower quartile and the median in grasslands, these values being lower than the global cropland median.

6.4 Discussion

6.4.1 A relatively homogeneous P status

All the sites, both aspen forest and grassland, presented a similar distribution of the P pools throughout the soil profile. Total P concentrations decreased with depth, mainly in relation to the decrease in the concentration of organic P (Table 6.2). The stock variation was of the same order of magnitude between and within sites and between contrasting vegetation cover types. The concentrations and the stocks we computed were close to those reported by Achat et al. (2013a). These authors reported standard errors of 1–27 % for the concentrations of total P, organic P, inorganic P, phosphate ions in soil solution and diffusive phosphate ions, with three replicates per condition at two sites of the same region. Assuming a similar spatial variability, the concentrations and stocks we measured or computed for given soil layers appeared relatively homogeneous (values of the same order of magnitude without notable outliers) on the regional scale.

Despite lower concentrations of the P pools in the subsoil, this contributed the most to the total stocks computed over 1 m (Table 6.3) because of its greater thickness. For the same reason, on the soil profile scale, inorganic P represented far more than 50 % of the total P stock (Table 6.3) while organic P concentrations represented a high proportion of total P in the litter and in the three first soil layers (Table 6.2). For the whole profile, the P stock in the soils studied can be qualified as predominantly

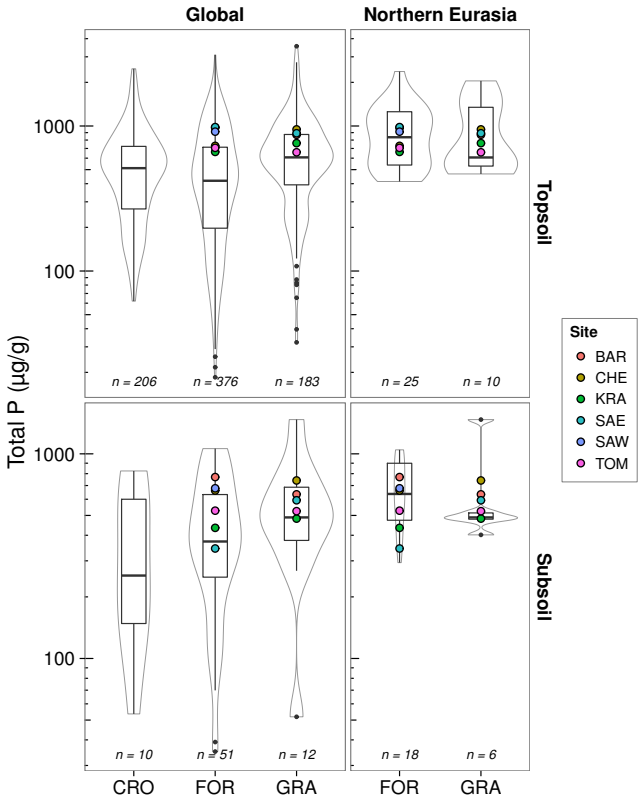


Figure 6.3: Comparison of total P concentrations in topsoils (about 0 to −20 cm) and subsoils (−20 to −100 cm depth) of south-western Siberia (coloured dots) with similar vegetation contexts (CRO: croplands; FOR: forests; GRA: grasslands) on the global scale and on the Northern Eurasian scale (box and violin plots). The "n" provided indicates the number of individual points used to build the box and the violin plots.

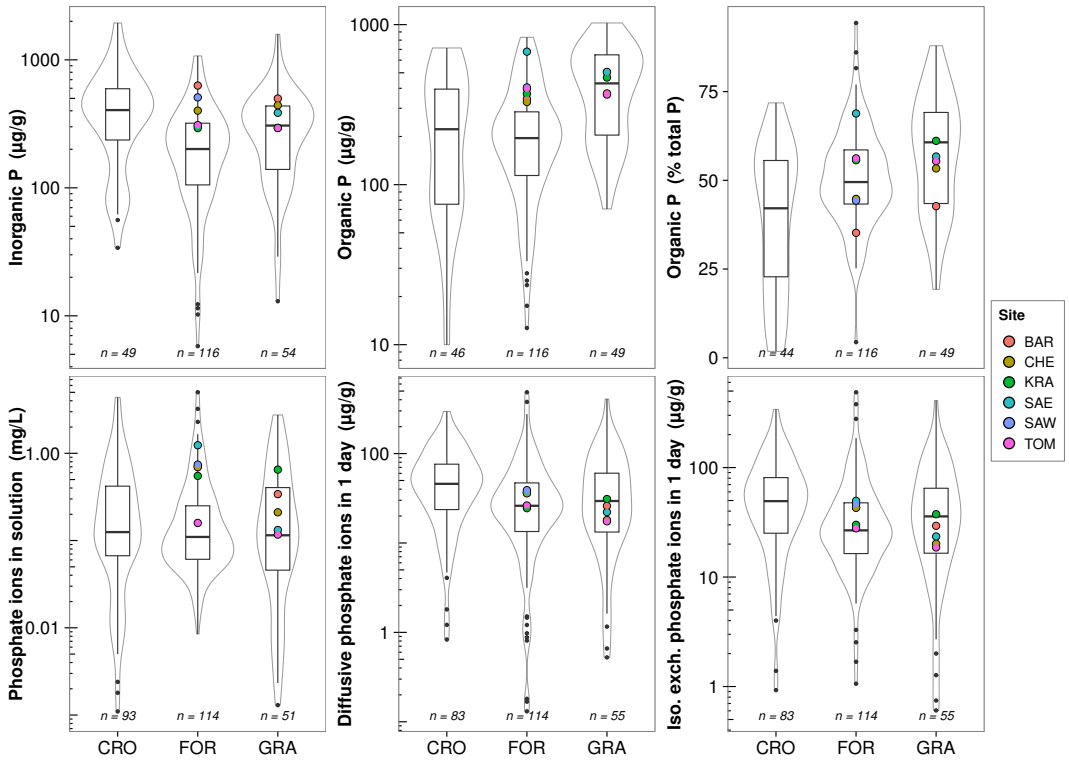


Figure 6.4: Comparison of the different components of the P status in topsoils (about 0 to −20 cm) of south-western Siberia (coloured dots) and different vegetation types (CRO: croplands; FOR: forests; GRA: grasslands—box and violin plots) on the global scale (croplands and grasslands) or on the country scale (forests mostly located in France, along broad gradients of soil and geology). "Iso. exch." is an abbreviation for "isotopically exchangeable". The "n" provided indicates the number of individual points used to build the box and the violin plots.

mineral down to 1 m.

6.4.2 Environmental factors controlling the regional P status

In spite of small variations in the current P status of the soils investigated, we found that this status was impacted by a set of variables. At first, we observed that the amount of P was highly dependent on the amount of inorganic P, particularly in the subsurface layers of the sites studied (Fig. 6.2 and Table 6.3). Biogeochemical cycling and soil development processes explain the P status with depth. In the topsoil, organic P represented a large part of total P (Fig. 6.2) and was related to organic C (Table D.6 and Fig. D.3). This is a direct consequence of P uptake, immobilization in plant tissues, followed by litterfall and subsequent accumulation in the top horizons (Barber 1995). Clay minerals (on their edges), carbonates and organic matter have surfaces presenting positive charges that are reactive with phosphate ions (Gérard 2016; Hinsinger 2001; Parfitt 1978). In the topsoil, the preponderance of organic P suggests that microbial processes may play an important role in the plant availability of P through the release of phosphate ions by mineralization. Conversely, in deep horizons P plant availability is principally explained by mineral phases such as the clay fraction (Table D.6 and Fig. D.3). Contrary to other case studies (Achat et al. 2011; do Carmo Horta and Torrent 2007; Tran et al. 1988; Walbridge et al. 1991), we found only a few relationships with Al and Fe oxides concentrations. These oxides also present positive charges that are known to be reactive with phosphate ions (Achat et al. 2011; Regelink et al. 2015).

The inspection of the correlations involving the parameters m and n provides further insights into the drivers of phosphate ion exchange at the solid–solution interface. Correlations with m, which is the fraction of radioactivity remaining after 1 min in the isotopic dilution, give information about rapid processes, while correlations with n are considered to be indicative of processes driving slow exchange reactions. Both parameters were related to the phosphate concentration in solution (Qw). Generally m increased with Qw while n decreased (Table D.6 and Fig. D.3), in agreement with previous studies (Achat et al. 2013a; Achat et al. 2009; Fardeau 1993; Morel et al. 2000). The dynamics of phosphate ions (slow reactions in the present study) were also dependent on pH, which modifies the charge of reactive solid surfaces and the speciation of phosphate ions (Barrow 1983; Hinsinger 2001; Strauss et al. 1997a,b; Ziadi et al. 2013). In addition, we found slight secondary effects of Al and Fe oxides on slow phosphate ion exchange reactions: residual values of the parameter n increased with the increase in oxide contents (data not shown). This is in accordance with a preliminary study in SW Siberia (see more details on the effects of Al and Fe oxides on parameter n in Achat et al. 2013a).

Nevertheless, at some sites, a few layers did not exhibit the general features of the P status described above. Soil formation processes and soil physico-chemical

properties also explain that we observed such "outliers". Despite overall slight effects only, soil content in Al and Fe oxides had some visible influence on soil P on the scale of some soil profiles. It was the case at TOM, a site with a water table close to the topsoil. The periodical water table movements may be responsible for the relatively stronger accumulation of clays and oxides in deeper soil layers (Table D.4) and contribute to the higher concentrations and proportions of diffusive phosphate ions of the soil (especially at −60 cm in grassland; Table D.4). At KRA, the accumulation of $CaCO_3$ (Table D.4) could be responsible for high levels of diffusive phosphate ions in the subsoil. In fact, in alkaline soils such as at KRA, phosphate ions tend to precipitate with Ca cations which have an increasing solubility at pHs above 8 (Hinsinger 2001; Kuo and Lotse 1972). At SAE, the schist material underlying the loess deposit (below −80 cm) is probably responsible for low P pool concentrations (particularly in forest) and extremely low proportions of diffusive phosphate ions in the deep layers compared with the other sites.

The restricted number of significant correlations—between P pools or isotopic dilution parameters (m and n) and soil physico-chemical properties—we identified in our study is not necessarily indicative of an absence of control of the P status. It may simply reflect that the values of the soil variables tested and P pool fall within a restricted range (with differences of only up to 1 order of magnitude; Table 6.2 and Table D.4). Soils of the SW part of Siberia are indeed relatively homogeneous. They have developed on loess material deposited during the Quaternary era, mainly during the two last glaciation periods (Chlachula 2003; Muhs 2007) and despite some contrasting climatic conditions, they have not been sufficiently impacted by diverging pedogenetic processes. Additionally, soil-forming processes are expected to be relatively slow in such a dry and cold region (Jenny 1941).

6.4.3 High levels of total P fractions but moderate ones for plant-available P

In general, the SW Siberian soils studied presented very high concentrations (above the third quartile) for total P, organic P, inorganic P and phosphate ions in soil solutions in forest and high concentrations (close to the third quartile) in grassland, when compared with our compilation of data on the global scale (or diverse soil and geological contexts mainly in France, for all P pools but total, P in forests) (Fig. 6.3 and 6.4). In addition, it might be possible to generalize the high level of total P stocks to Northern Eurasia, at least for the soils developed in the loess belt. Of course, more field measurements are required to verify this statement, particularly in the vast zone currently covered by taiga and not in the loess belt. On the other hand, this result, if confirmed, would be of primary importance in the context of global change and of tensions related to resources of P for agriculture.

However, we noted that these relatively high concentrations of total P in SW Siberian soils did not automatically indicate a high P availability for plant nutrition. In fact, an important parameter is the ability of the soil to refill a depleted soil solution (e.g. due to root uptake) with phosphate ions. This P buffering capacity assimilates the quantity of diffusive phosphate ions between the solid and the liquid phases of soil. Contrary to the other measured P pools in the SW Siberian soils studied, the concentrations of diffusive phosphate ions in the topsoil were not that high, in comparison with global levels (although not very low; Fig. 6.4).

In French forests, the sums of Al and Fe oxides range from 4.5 to 1157.7 mmol kg^{-1} and pHs range from 3.6 to 8.3 (data compilation of 106 sites, unpublished). In comparison, the SW Siberian soils studied have low sums of Al and Fe oxides (68.44–184.08 mmol kg^{-1})—and the narrow range of values explains why we found only a few correlations between P pools and oxides—and very high pHs (5.37–7.16; Table D.4). This very high pH is probably partly responsible for a low reactivity of phosphate ions, notably because the number of positive charges decreases with increasing pH (Barrow 1983; Hinsinger 2001; Ziadi et al. 2013). Coupled with a low amount of oxides (i.e. fixation sites), this might explain the average values of diffusive (*Pr*) and isotopically exchangeable (*E*) phosphate ions in the SW Siberian soils studied while total pools were (very) high.

Following the conceptual model of (Walker and Syers 1976), which describes the changes in the forms and amounts of P pools with time, together with the comments we made in the sections above about the regional homogeneity of the P status, we concluded that these SW Siberian soils are probably in the early stages of soil development. This stage is characterized by the build-up of an appreciable organic P stock but also by a stock of primary inorganic P which remains large and is made available by weathering. Thus, there may still be a high potential of primary mineral weathering in these soils. Moreover, the mineralization of organic matter is another source of phosphate ions available to refill the soil P buffering capacity (Achat et al. 2013b; Bünemann 2015). The study of the kinetics of these mechanisms is relatively difficult and was not carried out within the scope of this study. However, they could be of importance, as they are likely to be impacted by global change. Organic matter mineralization would mainly depend on temperature and moisture (Bengtson et al. 2005; Paul et al. 2002). Mineral alteration would mainly depend on temperature and pH (Augusto et al. 2000; Drever 1994).

The absence of correlation between fine-root densities and P pools (Table D.6) suggests that root exploration is not related to a search for P. In addition, the relatively low N:P ratios measured in the litter layers (9–14; Table D.4) as well as in aspen green leaves (9–12, data not shown) suggest that P is unlikely to be the primary limiting nutrient for plant nutrition and litter decomposition and that it could be N which may be the limiting factor (Aerts and Chapin 1999; Güsewell and Gessner 2009; Reich and Oleksyn 2004). Thus the availability of P probably

does not constrain plant growth in the ecosystems studied to any great extent. This conclusion is in line with the review by (Smurygin 1974) of fertilization experiments in the former USSR.

Will this P status be sufficient to fulfil future plant requirements in the context of global change? In the speculative situation where topsoils are depleted by intense biomass exports, our results suggest that the large P stocks in deeper soil layers could sustain the demand (Table 6.3). This would imply a deepening of plant fine-root systems, which has already been observed with ongoing global change, related to the increase in atmospheric CO_2 concentrations (Iversen 2010) or to the lengthening of vegetation growing seasons (Lempereur et al. 2015; Majdi and Öhrvik 2004). In SW Siberia, we suggest that deeper fine-root systems would be more likely to be driven by other resources, in particular water, in the steppe and forest-steppe zones (Brédoire et al. 2016b, Chap. 5).

6.5 Conclusions

This study revealed that the concentrations, the stocks of the different P pools measured and their distribution in the soil profile were relatively homogeneous on the scale of SW Siberia although there were some differences between sites (mainly organic P) possibly due to varying microbial activity and slight differences in physico-chemical soil properties. In this region, we argue that the young age of the soils developed on loess parent material, coupled with slow kinetics of pedogenesis, has probably not yet resulted in a sufficiently wide range of soil physico-chemical conditions to observe more diverging P status. The comparison of these Siberian P levels with similar types of vegetation on the global scale revealed high to very high levels of total, organic and inorganic P in the topsoils. It would seem possible to generalize these results to Northern Eurasia, but additional measurements are required to verify this statement. The amount of plant-available P in topsoils, evaluated as isotopically exchangeable phosphate ions, was intermediate on the global scale. However, large stocks of isotopically exchangeable phosphate ions are stored in the subsurface layers where fine-root exploration is currently low. These results suggest that the P resource is unlikely to constrain vegetation growth and agricultural development under present conditions and in the near future.

Author contribution

F. Brédoire, M. R. Bakker, P. A. Barsukov, B. Zeller and D. Derrien designed the sampling. F. Brédoire, M. R. Bakker, P. A. Barsukov, P. Nikitich and O. Rusalimova selected sites and performed the field work. F. Brédoire and D. L. Achat performed

laboratory measurements and analysed the data. F. Brédoire prepared the manuscript with contributions from D. L. Achat, M. R. Bakker, L. Augusto and D. Derrien. All co-authors revised the manuscript.

Acknowledgements

We thank the anonymous reviewers who contributed to the improvement of this manuscript by their comments and suggestions during the whole review process for *Biogeosciences Discussions*. We are grateful to all the people who helped in the field in July 2013, notably A. Bashuk, N. Gaberman, N. Kolosov, A. Litvinov, J. Petrashova, H. Rieckh, and A. Stupak. N. Gallegos (INRA Bordeaux) carried out part of the chemical analyses. B. Boitte and C. Tang (INRA Versailles) as well as M.-H. Bridet and M. Valentin (INRA Bordeaux) provided support in the search for articles from the journals *Soviet Soil Science* and *Eurasian Soil Science*. J. Regan suggested the title. The UR BEF and UMR ISPA are supported by the French National Research Agency through the Cluster of Excellence ARBRE (ANR-11-LABX-0002-01) and COTE (ANR-10-LABX-45), respectively. The project was funded by INRA Métaprogramme ACCAF and ERA.Net RUS.

References

Achat, D. L., Bakker, M. R., Augusto, L., Derrien, D., Gallegos, N., Lashchinskiy, N., Milin, S., Nikitich, P., Raudina, T., Rusalimova, O., Zeller, B., and Barsukov, P. (2013a). Phosphorus status of soils from contrasting forested ecosystems in southwestern Siberia: effects of microbiological and physicochemical properties. *Biogeosciences* 10.2, 733–752. DOI: 10.5194/bg-10-733-2013.

Achat, D. L., Augusto, L., Morel, C., and Bakker, M. R. (2011). Predicting available phosphate ions from physical-chemical soil properties in acidic sandy soils under pine forests. *Journal of Soils and Sediments* 11 (3), 452–466. DOI: 10.1007/s11368-010-0329-9.

Achat, D. L., Bakker, M. R., Augusto, L., and Morel, C. (2013b). Contributions of microbial and physical-chemical processes to phosphorus availability in Podzols and Arenosols under a temperate forest. *Geoderma* 211-212, 18–27. DOI: 10.1016/j.geoderma.2013.07.003.

Achat, D. L., Bakker, M. R., Augusto, L., Saur, E., Dousseron, L., and Morel, C. (2009). Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods. *Biogeochemistry* 92 (3), 183–200. DOI: 10.1007/s10533-008-9283-7.

Aerts, R. and Chapin, F. (1999). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. In: *Advances in Ecological Research*, 1–67. DOI: 10.1016/s0065-2504(08)60016-1.

AFNOR (1999). Qualité des sols. In: *Recueil de normes*. Vol. 1.

Ågren, G. I., Wetterstedt, J. Å. M., and Billberger, M. F. K. (2012). Nutrient limitation on terrestrial plant growth - modeling the interaction between nitrogen and phosphorus. *New Phytologist* 194.4, 953–960. DOI: 10.1111/j.1469-8137.2012.04116.x.

Augusto, L., Turpault, M.-P., and Ranger, J. (2000). Impact of forest tree species on feldspar weathering rates. *Geoderma* 96.3, 215–237. DOI: 10.1016/s0016-7061(00)00021-5.

Barber, S. A. (1995). Soil nutrient bioavailability – A mechanistic approach. In: 2nd. Chap. 9: Phosphorus, 201–228.

Barrow, N. J. (1983). A mechanistic model for describing the sorption and desorption of phosphate by soil. *The Journal of Soil Science* 34.4, 733–750. DOI: 10.1111/j.1365-2389.1983.tb01068.x.

Bengtson, P., Falkengren-Grerup, U., and Bengtsson, G. (2005). Relieving substrate limitation-soil moisture and temperature determine gross N transformation rates. *Oikos* 111.1, 81–90. DOI: 10.1111/j.0030-1299.2005.13800.x.

Bergen, K. M., Hitztaler, S. K., Kharuk, V. I., Krankina, O. N., Loboda, T. V., Zhao, T., Shugart, H. H., and Sun, G. (2012). Human dimensions of environmental change in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*, 251–302. DOI: 10.1007/978-94-007-4569-8_7.

Bünemann, E., Marschner, P., McNeill, A., and McLaughlin, M. (2007). Measuring rates of gross and net mineralisation of organic phosphorus in soils. *Soil Biology and Biochemistry* 39.4, 900–913. DOI: 10.1016/j.soilbio.2006.10.009.

Bünemann, E. K. (2015). Assessment of gross and net mineralization rates of soil organic phosphorus – A review. *Soil Biology and Biochemistry* 89, 82–98. DOI: 10.1016/j.soilbio.2015.06.026.

Černohlávková, J., Jarkovský, J., Nešporová, M., and Hofman, J. (2009). Variability of soil microbial properties: Effects of sampling, handling and storage. *Ecotoxicology and Environmental Safety* 72.8, 2102–2108. DOI: 10.1016/j.ecoenv.2009.04.023.

Chapman, P. J., Shand, C. A., Edwards, A. C., and Smith, S. (1997). Effect of storage and sieving on the phosphorus composition of soil solution. *Soil Science Society of America Journal* 61.1, 315–321. DOI: 10.2136/sssaj1997.03615995006100010045x.

Chlachula, J. (2003). The Siberian loess record and its significance for reconstruction of Pleistocene climate change in north-central Asia. *Quaternary Science Reviews* 22.18-19, 1879–1906. DOI: 10.1016/s0277-3791(03)00182-3.

Cooper, J., Lombardi, R., Boardman, D., and Carliell-Marquet, C. (2011). The future distribution and production of global phosphate rock reserves. *Resources, Conservation and Recycling* 57, 78–86. DOI: 10.1016/j.resconrec.2011.09.009.

Cordell, D., Rosemarin, A., Schröder, J., and Smit, A. (2011). Towards global phosphorus security: A systems framework for phosphorus recovery and reuse options. *Chemosphere* 84.6. The Phosphorus Cycle, 747–758. DOI: 10.1016/j.chemosphere.2011.02.032.

Cordell, D., Drangert, J.-O., and White, S. (2009). The story of phosphorus: Global food security and food for thought. *Global Environmental Change* 19.2. Traditional Peoples and Climate Change, 292–305. DOI: 10.1016/j.gloenvcha.2008.10.009.

do Carmo Horta, M. and Torrent, J. (2007). Phosphorus desorption kinetics in relation to phosphorus forms and sorption properties of Portuguese acid soils. *Soil Science* 172.8, 631–638. DOI: 10.1097/ss.0b013e3180577270.

Drever, J. I. (1994). The effect of land plants on weathering rates of silicate minerals. *Geochimica et Cosmochimica Acta* 58.10, 2325–2332. DOI: 10.1016/0016-7037(94)90013-2.

Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10.12, 1135–1142. DOI: 10.1111/j.1461-0248.2007.01113.x.

Fardeau, J. (1993). Le phosphore assimilable des sols : sa représentation par un modèle fonctionnel à plusieurs compartiments. *Agronomie* 13.4, 317–331. DOI: 10.1051/agro:19930409.

Fardeau, J. (1996). Dynamics of phosphate in soils. An isotopic outlook. *Fertilizer Research* 45.2, 91–100. DOI: 10.1007/bf00790658.

Fardeau, J.-C., Morel, C., and Boniface, R. (1991). Cinétique de transfer des ions phosphate diu sol vers la solution du sol: paramètres caractéristiques. *Agronomie* 11, 787–797.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., III, F. S. C., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F., and Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4.6, 471–476. DOI: 10.1038/nclimate2177.

Filippelli, G. M. (2008). The global phosphorus cycle: Past, present, and future. *Elements* 4.2, 89–95. DOI: 10.2113/gselements.4.2.89.

Frossard, E. and Sinaj, S. (1997). The isotope exchange kinetic technique: A method to describe the availability of inorganic nutrients. Applications to K, P, S and Zn. *Isotopes in Environmental and Health Studies* 33.1-2, 61–77. DOI: 10.1080/10256019808036360.

Frossard, E., Achat, D. L., Bernasconi, S. M., Bünemann, E. K., Fardeau, J.-C., Jansa, J., Morel, C., Rabeharisoa, L., Randriamanantsoa, L., Sinaj, S., Tamburini, F., and Oberson, A. (2011). The use of tracers to investigate phosphate cycling in soil–plant systems. In: *Phosphorus in Action*. Vol. 100, 59–91. DOI: 10.1007/978-3-642-15271-9_3.

Gérard, F. (2016). Clay minerals, iron/aluminum oxides, and their contribution to phosphate sorption in soils – A myth revisited. *Geoderma* 262, 213–226. DOI: 10.1016/j.geoderma.2015.08.036.

Giesler, R., Petersson, T., and Högberg, P. (2002). Phosphorus limitation in boreal forests: Effects of aluminum and iron accumulation in the humus layer. *Ecosystems* 5.3, 300–314. DOI: 10.1007/s10021-001-0073-5.

Gordov, E. P. and Vaganov, E. A. (2010). Siberia integrated regional study: multidisciplinary investigations of the dynamic relationship between the Siberian environment and global climate change. *Environmental Research Letters* 5.1, 015007. DOI: 10.1088/1748-9326/5/1/015007.

Groisman, P. Y., Blyakharchuk, T. A., Chernokulsky, A. V., Arzhanov, M. M., Marchesini, L. B., Bogdanova, E. G., Borzenkova, I. I., Bulygina, O. N., Karpenko, A. A., Karpenko, L. V., Knight, R. W., Khon, V. C., Korovin, G. N., Meshcherskaya, A. V., Mokhov, I. I., Parfenova,

E. I., Razuvaev, V. N., Speranskaya, N. A., Tchebakova, N. M., and Vygodskaya, N. N. (2012). Climate changes in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 3, 57–109. DOI: 10.1007/978-94-007-4569-8_3.

Groisman, P. and Soja, A. J. (2009). Ongoing climatic change in Northern Eurasia: justification for expedient research. *Environmental Research Letters* 4.4, 045002. DOI: 10.1088/1748-9326/4/4/045002.

Güsewell, S. (2004). N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164.2, 243–266. DOI: 10.1111/j.1469-8137.2004.01192.x.

Güsewell, S. and Gessner, M. O. (2009). N : P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. *Functional Ecology* 23.1, 211–219. DOI: 10.1111/j.1365-2435.2008.01478.x.

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B., and Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters* 14.9, 852–862. DOI: 10.1111/j.1461-0248.2011.01651.x.

He, M. and Dijkstra, F. A. (2014). Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytologist* 204.4, 924–931. DOI: 10.1111/nph.12952.

Hedin, L. O. (2004). Global organization of terrestrial plant-nutrient interactions. *Proceedings of the National Academy of Sciences* 101.30, 10849–10850. DOI: 10.1073/pnas.0404222101.

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* 237.2, 173–195. DOI: 10.1023/A:1013351617532.

IPCC (2013). *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Ed. by T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. Midgley. Cambridge Books Online. Cambridge University Press. 1535 pp. DOI: 10.1017/CBO9781107415324.

IUSS Working Group WRB (2014). *World Reference Base for Soil Resources 2014 - International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106*. FAO.

Iversen, C. M. (2010). Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. *New Phytologist* 186.2, 346–357. DOI: 10.1111/j.1469-8137.2009.03122.x.

Jenny, H. (1941). Factors of soil formation. *Soil Science* 52.5, 415. DOI: 10.1097/00010694-194111000-00009.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J. (2012). Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. *Ecology and Evolution* 2.3, 593–614. DOI: 10.1002/ece3.85.

Kicklighter, D. W., Cai, Y., Zhuang, Q., Parfenova, E. I., Paltsev, S., Sokolov, A. P., Melillo, J. M., Reilly, J. M., Tchebakova, N. M., and Lu, X. (2014). Potential influence of climate-induced

vegetation shifts on future land use and associated land carbon fluxes in Northern Eurasia. *Environmental Research Letters* 9.3, 035004. DOI: 10.1088/1748-9326/9/3/035004.

Kuo, S. and Lotse, E. G. (1972). Kinetics of phosphate adsorption by calcium carbonate and Ca-kaolinite1. *Soil Science Society of America Journal* 36.5, 725–729. DOI: 10.2136/sssaj1972.03615995003600050015x.

Lempereur, M., Martin-StPaul, N. K., Damesin, C., Joffre, R., Ourcival, J.-M., Rocheteau, A., and Rambal, S. (2015). Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: implications for assessing forest productivity under climate change. *New Phytologist* 207.3, 579–590. DOI: 10.1111/nph.13400.

MacDonald, G. K., Bennett, E. M., Potter, P. A., and Ramankutty, N. (2011). Agronomic phosphorus imbalances across the world's croplands. *Proceedings of the National Academy of Sciences* 108.7, 3086–3091. DOI: 10.1073/pnas.1010808108.

Majdi, H. and Öhrvik, J. (2004). Interactive effects of soil warming and fertilization on root production, mortality, and longevity in a Norway spruce stand in Northern Sweden. *Global Change Biology* 10.2, 182–188. DOI: 10.1111/j.1365-2486.2004.00733.x.

McKeague, J. A. and Day, J. H. (1966). Dithionite and oxalate-extractable Fe and Al as aids in differentiating various classes of soils. *Canadian Journal of Soil Science* 46.1, 13–22. DOI: 10.4141/cjss66-003.

Miller, A. J., Schuur, E. A., and Chadwick, O. A. (2001). Redox control of phosphorus pools in Hawaiian montane forest soils. *Geoderma* 102.3-4, 219–237. DOI: 10.1016/s0016-7061(01)00016-7.

Mooney, H. A., Drake, B. G., Luxmoore, R. J., Oechel, W. C., and Pitelka, L. F. (1991). Predicting ecosystem responses to elevated CO_2 concentrations. *BioScience* 41.2, 96–104. DOI: 10.2307/1311562.

Morel, C. and Plenchette, C. (1994). Is the isotopically exchangeable phosphate of a loamy soil the plant-available P? *Plant and Soil* 158.2, 287–297. DOI: 10.1007/bf00009502.

Morel, C., Tunney, H., Plénet, D., and Pellerin, S. (2000). Transfer of phosphate ions between soil and solution: Perspectives in soil testing. *Journal of Environmental Quality* 29.1, 50–59. DOI: 10.2134/jeq2000.00472425002900010007x.

Muhs, D. (2007). Loess deposits, origins and properties. In: *Encyclopedia of Quaternary Science*, 1405–1418. DOI: 10.1016/b0-44-452747-8/00158-7.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R. (2005). Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* 102.50, 18052–18056. DOI: 10.1073/pnas.0509478102.

Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schafer, K. V., McCarthy, H., Hendrey, G., McNulty, S. G., and Katul, G. G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature* 411.6836, 469–472. DOI: 10.1038/35078064.

Parfitt, R. (1978). Anion adsorption by soils and soil materials. In: *Advances in Agronomy*. Vol. 30, 1–50. DOI: 10.1016/s0065-2113(08)60702-6.

Paul, K. I., Polglase, P. J., O'Connell, A. M., Carlyle, J. C., Smethurst, P. J., and Khanna, P. K. (2002). Soil nitrogen availability predictor (SNAP): a simple model for predicting mineralisation of nitrogen in forest soils. *Australian Journal of Soil Research* 40.6, 1011–1026. DOI: 10.1071/sr01114.

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., Velde, M. van der, Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M., and Janssens, I. A. (2013). Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications* 4. DOI: 10.1038/ncomms3934.

Peñuelas, J., Sardans, J., Rivas-ubach, A., and Janssens, I. A. (2012). The human-induced imbalance between C, N and P in Earth's life system. *Global Change Biology* 18.1, 3–6. DOI: 10.1111/j.1365-2486.2011.02568.x.

R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Regelink, I. C., Weng, L., Lair, G. J., and Comans, R. N. J. (2015). Adsorption of phosphate and organic matter on metal (hydr)oxides in arable and forest soil: a mechanistic modelling study. *European Journal of Soil Science* 66.5, 867–875. DOI: 10.1111/ejss.12285.

Reich, P. B. and Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences* 101.30, 11001–11006. DOI: 10.1073/pnas.0403588101.

Reich, P. B., Hobbie, S. E., and Lee, T. D. (2014). Plant growth enhancement by elevated CO_2 eliminated by joint water and nitrogen limitation. *Nature Geoscience* 7.12, 920–924. DOI: 10.1038/ngeo2284.

Reich, P. B., Hobbie, S. E., Lee, T., Ellsworth, D. S., West, J. B., Tilman, D., Knops, J. M. H., Naeem, S., and Trost, J. (2006a). Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature* 440.7086, 922–925. DOI: 10.1038/nature04486.

Reich, P. B., Hungate, B. A., and Luo, Y. (2006b). Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution, and Systematics* 37.1, 611–636. DOI: 10.1146/annurev.ecolsys.37.091305.110039.

Saunders, W. M. H. and Williams, E. G. (1955). Observations on the determination of total organic phosphorus in soils. *The Journal of Soil Science* 6.2, 254–267. DOI: 10.1111/j.1365-2389.1955.tb00849.x.

Schimel, D. S. (1995). Terrestrial ecosystems and the carbon cycle. *Global Change Biology* 1.1, 77–91. DOI: 10.1111/j.1365-2486.1995.tb00008.x.

Shiklomanov, A. I. and Lammers, R. B. (2009). Record Russian river discharge in 2007 and the limits of analysis. *Environmental Research Letters* 4.4, 045015. DOI: 10.1088/1748-9326/4/4/045015.

Shkolnik, I. M., Nadyozhina, E. D., Pavlova, T. V., Molkentin, E. K., and Semioshina, A. A. (2010). Snow cover and permafrost evolution in Siberia as simulated by the MGO regional climate model in the 20th and 21st centuries. *Environmental Research Letters* 5.1, 015005. DOI: 10.1088/1748-9326/5/1/01500510.1088/1748-9326/5/1/015005.

Shuman, J. K., Tchebakova, N. M., Parfenova, E. I., Soja, A. J., Shugart, H. H., Ershov, D., and Holcomb, K. (2015). Forest forecasting with vegetation models across Russia. *Canadian Journal of Forest Research* 45.2, 175–184. DOI: 10.1139/cjfr-2014-0138.

Smurygin, M. (1974). Basic trends of grassland research in the USSR. In: *Proceedings of the 12th International Grassland Congress. Moscow, Russia, 11–24 June 1974*, 76–88.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S., and Stackhouse Jr., P. W. (2007). Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56.3–4, 274–296. DOI: 10.1016/j.gloplacha.2006.07.028.

Strauss, R., Brummer, G., and Barrow, N. (1997a). Effects of crystallinity of goethite: I. Preparation and properties of goethites of differing crystallinity. *European Journal of Soil Science* 48.1, 87–99. DOI: 10.1111/j.1365-2389.1997.tb00188.x.

Strauss, R., Brummer, G., and Barrow, N. (1997b). Effects of crystallinity of goethite: II. Rates of sorption and desorption of phosphate. *European Journal of Soil Science* 48.1, 101–114. DOI: 10.1111/j.1365-2389.1997.tb00189.x.

Sundqvist, M. K., Wardle, D. A., Vincent, A., and Giesler, R. (2014). Contrasting nitrogen and phosphorus dynamics across an elevational gradient for subarctic tundra heath and meadow vegetation. *Plant and Soil* 383.1-2, 387–399. DOI: 10.1007/s11104-014-2179-5.

Tchebakova, N. M., Parfenova, E. I., Lysanova, G. I., and Soja, A. J. (2011). Agroclimatic potential across central Siberia in an altered twenty-first century. *Environmental Research Letters* 6.4, 045207. DOI: 10.1088/1748-9326/6/4/045207.

Tchebakova, N. M., Parfenova, E., and Soja, A. J. (2009). The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4.4, 045013. DOI: 10.1088/1748-9326/4/4/045013.

Tchebakova, N. M., Rehfeldt, G. E., and Parfenova, E. I. (2010). From vegetation zones to climatypes: Effects of climate warming on Siberian ecosystems. In: *Permafrost Ecosystems. Siberian Larch Forests*. Chap. 22, 427–447.

Tran, T. S., Giroux, M., and Fardeau, J. C. (1988). Effects of soil properties on plant-available phosphorus determined by the isotopic dilution phosphorus-32 method. *Soil Science Society of America Journal* 52.5, 1383–1390. DOI: 10.2136/sssaj1988.03615995005200050033x.

van Groenigen, K.-J., Six, J., Hungate, B. A., de Graaff, M.-A., van Breemen, N., and van Kessel, C. (2006). Element interactions limit soil carbon storage. *Proceedings of the National Academy of Sciences* 103.17, 6571–6574. DOI: 10.1073/pnas.0509038103.

van Veldhoven, P. P. and Mannaerts, G. P. (1987). Inorganic and organic phosphate measurements in the nanomolar range. *Analytical Biochemistry* 161.1, 45–48. DOI: 10.1016/0003-2697(87)90649-x.

Vincent, A. G., Sundqvist, M. K., Wardle, D. A., and Giesler, R. (2014). Bioavailable Soil Phosphorus Decreases with Increasing Elevation in a Subarctic Tundra Landscape. *PLoS ONE* 9.3, e92942. DOI: 10.1371/journal.pone.0092942.

Vitousek, P. M., Porder, S., Houlton, B. Z., and Chadwick, O. A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications* 20.1, 5–15. DOI: 10.1890/08-0127.1.

Walbridge, M., Richardson, C., and Swank, W. (1991). Vertical distribution of biological and geochemical phosphorus subcycles in two southern Appalachian forest soils. *Biogeochemistry* 13.1, 61–85. DOI: 10.1007/bf00002876.

Walker, T. and Syers, J. (1976). The fate of phosphorus during pedogenesis. *Geoderma* 15.1, 1–19. DOI: 10.1016/0016-7061(76)90066-5.

Ziadi, N., Whalen, J. K., Messiga, A. J., and Morel, C. (2013). Assessment and modeling of soil available phosphorus in sustainable cropping systems. In: *Advances in Agronomy*, 85–126. DOI: 10.1016/b978-0-12-417187-9.00002-4.

Chapter 7

Decomposition of ^{15}N-labelled litter and fate of nitrogen derived from litter in aspen forests and grasslands of south-western Siberia

In collaboration with: D. Derrien, M. R. Bakker, P. A. Barsukov, A. Bashuk, Z. E. Kayler, P. Nikitich, O. Rusalimova, and B. Zeller.

7.1 Introduction

Nitrogen (N) is a major nutrient for all living organisms. It is often limiting the primary productivity of ecosystems, either alone or in combination with other nutrients such as phosphorus (Elser et al. 2007; Fay et al. 2015; Fernández-Martínez et al. 2014; Güsewell 2004; Harpole et al. 2011; Vitousek et al. 2010). There are three sources of N to ecosystems: rock N, atmospheric N, and N in organic matter. Rock N is usually considered as a marginal source of bio-available N. Some plants, e.g. legumes, assimilate atmospheric N through symbiosis with N-fixing micro-organisms. N from organic matter becomes available to plants through decomposition. In most ecosystems, organic N is the major source of bio-available N. The decomposition process consists in fragmentation, depolymerization and mineralization in the litter–soil organic matter continuum (Schimel and Bennett 2004). It is carried out by complex interactions between abiotic (light, wind, precipitation, freezing, etc.) and biotic factors (soil fauna, fungi and bacteria) which break down litter into smaller sized particles and soluble compounds (Berg and McClaugherty 2014). These products of litter decomposition are incorporated to the mineral soil and become soil organic matter (SOM). Depending on environmental conditions—such as soil properties, soil processes, biological activity and climate—SOM follows different pathways of mineralization and/or stabilization (Cotrufo et al. 2015; Lehmann and Kleber 2015; Schmidt et al. 2011; von Lützow et al. 2006). The degree and depth of incorporation of litter-derived organic matter into the soil, either as particulate organic matter or soluble compounds, mainly depends on the activity of the fauna, the leaching

intensity of solubles, the intensity of particle flow and the ability of the soil to retain SOM components both in space and time. Finally, the N derived from organic matter is taken up by plants in the soil solution either as small organic molecules (e.g. amino acids) or inorganic forms (ammonium, NH_4^+, and nitrate, NO_3^-) (Näsholm et al. 2009; Schimel and Bennett 2004).

The dynamics of N exhibit specific features in seasonally snow-covered regions (Brooks et al. 2011). First, during winter, the snow-pack modulates soil temperature. A thick snow-pack protects soil from freezing due to insulating properties (Zhang 2005). However, when the permanent snow cover appears late, soil can already be frozen and remain as such over winter. In unfrozen soils, biological activity is maintained at a basal level during winter (Monson et al. 2006b). In contrast, when the soil freezes, microbial cells are lyzed, what drastically decreases the size of the population and releases soluble microbial N in the soil (Henry 2007). Secondly, the period of snow-melt and soil warming is of great importance. Most of the soil water recharge and nutrient leaching can occur during this time (Chap. 4; Campbell et al. 2014a; Sebestyen et al. 2008; Sickman et al. 2003). In the case where microbial communities were impacted by soil freezing, soluble microbial N had been released in winter and could be exported from the system at snow-melt (Brooks et al. 2011; Henry 2007). In addition, the stimulation of microbial activity due to the rising of soil temperature would be delayed compared with unfrozen soil, the time for the microbial community to grow.

There is increasing interest in Siberian ecosystems in the context of global change (Groisman and Gutman 2012). Additional insights on biogeochemical cycles are required, especially on N cycling. In this study, we propose to investigate the fate of N released from decaying leaf-litter in south-western (SW) Siberia. SW Siberia is positioned on gradient of climate, soil and vegetation. In the south, typically in steppe/forest-steppe, soil experiences freezing over winter, because of a relatively shallow snow-pack, and water shortages are frequent in summer (Chap. 3 and 4). In the north, typically in sub-taiga, the soil is barely frozen in winter due a thick snow-pack and soil moisture content is not limiting in summer. From its position in Northern Eurasia, SW Siberia is submitted to a particularly intense climate change. In particular, temperatures are rising and winter precipitations are increasing, thus snow height (Bulygina et al. 2011, 2010, 2009; Groisman et al. 2012; IPCC 2013).

In this study, we posit that N cycling strongly differs between the north and the south of SW Siberia due to contrasting climatic conditions. We hypothesize that in the north, the cycling of N in the soil–plant system is faster than in the south. It is based on the assumption that, in the north, decomposition processes and N release from organic matter would not be limited by summer drought, and would increase very fast at spring when plants require nutrients because a minimal microbial activity would have been mantained in winter.

Our experimental approach was to track leaf-derived N over time in the soil–plant

continuum using ^{15}N labelling. ^{15}N-labelled litter is a valuable tool to study N cycling in various ecosystem compartments (litter, fauna, soil, micro-organisms, plants) on the long-term and with little disturbance of natural processes. For example, it was employed in diverse forest ecosystems to study the redistribution and allocation within the soil–plant system of N derived from leaf-litter (Zeller et al. 2001, 2000) and harvest-residues (Blumfield et al. 2004; Versini et al. 2013), the acquisition of litter-N by fauna (Caner et al. 2004) and fungi (Pena et al. 2013), and the stabilization of litter-N in SOM (Bimüller et al. 2013; Hatton et al. 2012, 2015; Mambelli et al. 2011; Zeller and Dambrine 2011). In four sites chosen along a gradient of climate, we applied ^{15}N-labelled leaf litter on the soil surface and, during three years, we monitored the redistribution of ^{15}N within litter, soil and herbaceous vegetation. In each site, we set up experimental plots in an aspen forest and in a grassland. ^{15}N derived from the decomposing labelled-litter was tracked twice a year in the organic layers, in the first 15 cm, and in above-ground vegetation.

7.2 Materials and methods

7.2.1 Site description

We selected four sites in SW Siberia on a transition from the forest-steppe to the sub-taiga bioclimatic zones. Barnaul (BAR) is located in the southern part of the forest-steppe bioclimatic zone, Salair East (SAE) on the transition between sub-taiga and forest-steppe in the foothills of the Salair mountains range, Salair West (SAW) in the "Blackish" taiga belt of Salair mountains, and Tomsk (TOM) in sub-taiga. Sites located in the forest-steppe are expected to be drier, to have higher mean temperature and to experience a lower height of snow during winter than sites located in the sub-taiga (Table 7.1).

SW Siberia is located in the northern part of the Eurasian loess belt, a broad area ranging from 40 to 60 °N latitude where soil present favourable texture and mineralogy for plant growth (Chlachula 2003; Muhs 2007). Since climatic conditions and vegetation cover differ in intensity essentially along a gradient from south to north, the soils in SW Siberia have undergone different development from their common origin as loess deposits. At BAR, and SAE, the main soil-forming processes are the formation and accumulation of organic matter, leaching of carbonates in the topsoil and formation of secondary carbonates in deep soil layers. Soils belong to the groups of Chernozems and Phaeozems (Table 7.1). At SAW and TOM the main soil-forming processes are related to the periodical movements of the water table, clays are washed from the topsoil and accumulate in the deeper layers and carbonates have disappeared from the first metre of the soil profile. In these two sites, soils belong to the group of Luvisols (Table 7.1). Fine root (< 0.8 mm diameter)

Table 7.1: Main characteristics of the study sites.

Site ID	BAR	SAE	SAW	TOM
General				
Site name	Barnaul	Salair East	Salair West	Tomsk
Bioclimatic zone	Forest-steppe	Sub-taiga to forest-steppe	"Blackish taiga"	Sub-taiga
Soil in forest	Haplic Phaeozem	Leptic Phaeozem	Haplic Luvisol	Albic Luvisol
Soil in grassland	Calcic Chernozem	Leptic Phaeozem		Albic Luvisol
Latitude N	53.41	54.39	54.18	56.3
Longitude E	83.47	85.75	85.17	85.43
Elevation (m asl)	221	305	358	232
Climatic features (average values over the period 1981–2010)				
WMO index[a]	29838	29745	29736	29430
Distance[b] (km)	4	18	64	38
Air temperature[c] (°C)	2.7	2.3	1.2	0.9
Precipitation[d] (mm)	432	432	453	567
Snow height[e] (cm)	49	38	54	71
Snow-pack > 1 cm (days)	157	145	149	178
Snow-pack > 20 cm (days)	108	88	116	145
Snow height during the investigated period of time: mean (min–max)[ef]				
Winter 2013–2014 forest	35.42 (20–46)[g]	na	na	63.66 (50–72)[h]
Winter 2013–2014 grassland	34.81 (23–47)[g]	na		57.92 (51–64)[h]
Winter 2014–2015 forest	84.17 (65–95)[i]	56.67 (50–70)[j]	112.08 (110–120)[j]	88.06 (80–90)[k]
Winter 2014–2015 grassland	58.42 (50–70)[i]	60.63 (50–70)[j]		78.21 (70–86)[k]

[a]World Meteorological Organization (WMO) index of the closest weather station; [b]distance site–weather station; [c]mean annual temperature; [d]mean annual precipitation; [e]snow height at climax (usually between mid-February and mid-March); [f]snow was measured on the experimental sites every meter with the help of a rigid ruler on a transect of 20 m; [g]22/02/2014; [h]15/02/2014; [i]24/02/2015; [j]25/02/2015; [k]27/02/2015

exploration occurs deeper in forest-steppe than in sub-taiga (Brédoire et al. 2016).

All the study sites had comparable features in terms of dominant species composition, stand characteristics and low human impact (i.e. no active management for the last decades; Tables E.2 and E.1). They had almost pure aspen (*Populus tremula* L.; Table E.2) forest stands along with nearby grassland areas. SAW did not present grassland areas. So there were four sites with forest and three with grassland in our data set for SW Siberia. All aspen stands had closed canopy.

7.2.2 Vegetation productivity estimation

Five litter-traps were set up in July 2013 on each of the four forested study sites. Each litter-trap was constituted by a nylon net with a mesh size of 1.5 cm. They were disposed on the ground over a surface area of 1.96 m^2 after vegetation removal. Leaf litter was collected after the fall of all leaves at the end of September–beginning of October. We removed branches and oven-dried the fresh litter at 60 °C to constant weight. Aliquots of this litter were analysed for total carbon (C) and nitrogen (N) concentration.

We followed the same procedure to sample herbaceous green vegetation in grasslands and in forests (understorey vegetation) in July 2013. A transect of 20 m was randomly defined and materialized with a rope in 3 replicate plots (spaced by 200–2000 m). The vegetation was cut every meter along these transects over a surface area of 30 cm by 40 cm delimited by a rigid frame. All the alive aboveground vegetation was collected without distinction between species. There were 10 samples per transect, so 30 per site. The samples were oven dried at 60 °C to constant weight.

7.2.3 Topsoil physico-chemical characterization

Most physico-chemical characterization of two topsoil layers, −5 and −15 cm ± 5 cm, was performed on composite samples established from three soil pits. Individual samples were air dried and sieved at 2 mm to remove stones and coarse roots before being pooled in a composite sample. Soil density samples (one per soil pit and per layer) were collected with a cylinder (97 cm^3). They were oven dried at 105 °C for 48 h and stones were removed when present. Apparent density was measured on each replicate (3 soils pits).

The French standard methods (Association Française de NORmalisation; AFNOR 1999) were used for most of the physico-chemical soil analyses. For soil texture, the five-size fractions for clay (< 2 µm diameter), fine loam (2–20 µm), coarse loam (20–50 µm), fine sand (50–200 µm), and coarse sand (200–2000 µm) were assessed after decarbonation (NF X 31–107). Soil pH–H_2O was determined in a water/soil suspension with a mass-to volume ratio of 1 g: 2.5 mL (NF ISO 10390). Total calcium carbonate contents were assessed with a volumetric method (NF X 31–105). Poorly

Table 7.2: Soil physico-chemical properties. Composite sample from 3 soil pits, except total C and total N which are means of all the samples analysed for ^{15}N isotopic composition ($n = 3 - -4$).

	Depth	Forest				Grassland		
	(cm)	BAR	SAE	SAW	TOM	BAR	SAE	TOM
Apparent density	5	1.0	0.5	0.7	0.9	1.0	0.9	0.9
	15	1.2	0.8	1.0	1.1	1.3	1.1	1.2
Granulo. 0–2 µm[a] (%)	5	27.7	40.7	22.2	23.2	27.5	35.3	22.0
	15	27.2	36.8	20.4	21.9	27.7	34.9	21.2
2–20 µm[a] (%)	5	23.2	26.5	37.9	38.8	20.7	23.8	38.9
	15	23.0	25.3	38.2	38.7	21.0	23.9	40.5
20–50 µm[a] (%)	5	35.3	14.9	34.4	30.2	35.5	17.0	30.8
	15	35.7	15.6	36.6	31.0	32.7	17.6	31.7
50–200 µm[a] (%)	5	13.0	4.4	4.6	6.9	14.0	4.7	6.7
	15	13.5	5.2	3.9	7.4	16.0	4.2	4.7
200–2000 µm[a] (%)	5	0.7	13.4	0.8	0.8	2.2	19.1	1.5
	15	0.5	17.0	0.8	0.9	2.5	19.3	1.8
pH H_2O	5	6.10	6.17	6.07	5.37	6.50	6.47	5.45
	15	6.12	5.97	5.45	5.25	7.20	6.58	5.54
Total N	0–2.5	5.51	8.76	5.83	5.70	4.81	7.78	3.77
(mg N g^{-1} dry soil)	2.5–5	4.25	7.41	4.41	5.02	3.07	5.47	3.01
	5–7.5	3.22	5.66	3.40	4.20	2.77	4.80	2.68
	7.5–10	3.02	4.72	2.67	3.73	2.70	4.59	2.35
	10–15	2.75	3.86	2.48	3.36	2.71	4.57	2.06
Total C	0–2.5	73.59	115.53	78.45	76.21	56.86	95.06	49.02
(mg C g^{-1} dry soil)	2.5–5	53.83	93.29	55.23	64.60	33.50	65.91	36.06
	5–7.5	39.66	72.95	39.13	50.91	30.64	57.67	29.37
	7.5–10	37.13	60.97	28.50	43.57	29.72	54.92	24.63
	10–15	33.54	53.01	26.28	38.08	29.55	54.44	21.10
Total $CaCO_3$	5	< 1	< 1	< 1	< 1	< 1	< 1	< 1
(g kg^{-1})	15	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Al oxides	5	63.4	101.6	77.1	86.7	58.6	101.2	90.4
(mmol kg^{-1})	15	64.9	126.0	88.9	95.3	59.3	104.9	91.2
Fe oxides	5	31.3	56.0	68.0	75.2	25.2	48.5	93.7
(mmol kg^{-1})	15	33.3	67.2	75.6	79.0	26.3	49.6	95.6
FRLD[bd]	5	1.44	2.16	0.92	0.77	2.35	2.82	2.79
(cm roots cm^{-3} soil)	15	0.77	0.94	0.37	0.82	1.30	1.03	1.06
FRMD[cd]	5	1.47	1.88	0.86	0.87	1.49	2.04	1.06
(mg roots cm^{-3} soil)	15	0.56	0.87	0.52	0.58	0.59	0.49	0.22

[a]granulometric fraction; [b]fine root length density; [c]fine root mass density;

[d]see Brédoire et al. 2016

Table 7.3: Characteristics of the ^{15}N-labelled litters deposited.

	BAR	SAE	SAW	TOM
Forest				
Date of deposition	26/09/2012	19/10/2012	30/09/2012	05/10/2012
Mass deposited (g m^{-2})	255	255	255	255
δ^{15}N (‰)	528	528	528	528
Abundance ^{15}N (atom %)	0.56	0.56	0.56	0.56
Total N (mg g^{-1})	13.23	13.23	13.23	13.23
Total C (mg g^{-1})	446.64	446.64	446.64	446.64
Grassland				
Date of deposition	25/09/2012	19/10/2012		06/10/2012
Mass deposited (g m^{-2})	204	306		357
δ^{15}N (‰)	3158.86	3158.86		3158.86
Abundance ^{15}N (atom %)	1.51	1.51		1.51
Total N (mg g^{-1})	9.90	9.90		9.90
Total C (mg g^{-1})	424.13	424.13		424.13

crystalline aluminium (Al) and iron (Fe) oxides were extracted with an ammonium oxalate solution (McKeague and Day 1966). Total C and N concentrations were measured along with the isotopic composition on all the samples related to the ^{15}N experiment (see below). The soil characteristics are presented in Table 7.2.

7.2.4 Temperature recording

From autumn 2012, both forests and grasslands were equipped with temperature data loggers (DS1921G Thermochron iButton, Maxim Integrated, USA). The data loggers were set up at three soil depths, −5, −15, and −60 cm in holes or tranches made with the help of a soil corer or a spade. Two to four replicates were set up per site and vegetation cover. One to two temperature data loggers were also set up at 2 m above the soil surface on each site and for each vegetation cover. The temperature data loggers were changed regularly (usually every 6 months).

7.2.5 Preparation and installation of ^{15}N-labelled litters

^{15}N-labelled aspen and grass leaf litters were produced near the village of Chebula (Novosibirsk region, in the middle of the transect of sites). ^{15}N-labelled urea was spread on the foliage of aspen trees and on alive grasses in late June 2012 (Zeller et al. 1998). These labelled materials were collected at the beginning of September 2012, in the late phase of senescence but before brown aspen leaves fall on the ground.

The collected material was air dried to avoid decomposition before its deposition on the experimental field sites.

In late September–beginning of October 2012, we deposited the ^{15}N-labelled litters on six experimental plots of 1.40 by 1.40 m per site and per vegetation cover (Table 7.3). The distance between two plots was approximately 3–15 m. In forest plots, we carefully removed fresh litterfall (fresh leaf litter and a few branches) over the area of the experimental plot and replaced it by an amount of ^{15}N-labelled aspen litter similar to the supposed production (500 g of dry ^{15}N-labelled litter, Table 7.3) evenly distributed over the plot area. In grassland plots, we cut and removed dead grasses and deposited a similar amount of ^{15}N-labelled grass litter (400, 600 and 700 g of dry ^{15}N-labelled litter at BAR, SAE and TOM, respectively, Table 7.3) evenly distributed over the plot area. The deposited labelled litters were fixed on the soil surface with a nylon net (mesh size of 1.5 cm) to avoid wind dispersal and contamination by non-labelled litter.

7.2.6 Samplings and analyses

From 2013 to 2015, we sampled vegetation (herbaceous species), litter and soil twice a year, at the end of Spring and in Autumn. All vegetation and litter layers—that is to say litter Ol above the net and, below the net, ^{15}N-labelled litter eventually remaining, litter Of, and litter Oh if present—were sampled over an area of 30 by 40 cm delimited by a rigid plastic frame. Five mineral soil layers were sampled on the same area using a knife and a spoon: 0–2.5 cm, 2.5–5 cm, 5–7.5 cm, 7.5–10 cm and 10–15 cm. Vegetation and litter samples were oven-dried at 60 °C and soil samples were air dried, all to constant weight. The soil was then sieved at 2 mm to remove roots (the topsoils studied do not present gravels). The samples were homogenized and an aliquot was finely ground before isotope analyses.

Elemental and isotopic compositions (total C, total N and ^{15}N abundance) were determined with an Elemental Analyser–Isotope Ratio Mass Spectrometer (EA–IRMS, Delta S, Thermo-Finnigan, Germany) using appropriate standards for normalization correction, instrument linearity, and precision purposes.

The ^{15}N natural abundance of vegetation, litter and of the five soil layers defined from 0 to 15 cm were measured at each site on material sampled in July 2013 and prepared following the same methods.

7.2.7 Isotopic computations

The isotopic composition of the samples was expressed in delta units (δ^{15}N, ‰):

$$\delta^{15}\mathrm{N} = 100 \times \left(\frac{\mathrm{R_{sample}} - \mathrm{R_{standard}}}{\mathrm{R_{standard}}} \right) \times 1000 \qquad (7.1)$$

where R is the mass ratio of ^{15}N to ^{14}N and $R_{standard}$ equals 0.0036765.

The proportion of ^{15}N in the total amount of N measured in a sample (N_{tot}), the ^{15}N abundance ($A^{15}N$, in %), was computed as following:

$$A^{15}N = \frac{^{15}N}{^{15}N + ^{14}N} = 100 \times \frac{\left(\frac{\delta^{15}N}{1000} + 1\right) \times R_{standard}}{\left[\left(\frac{\delta^{15}N}{1000} + 1\right) \times R_{standard}\right] + 1} \quad (7.2)$$

The proportion of ^{15}N tracer (i.e. the ^{15}N excess, $E^{15}N$, in %) in each sample was obtained by:

$$E^{15}N = A^{15}N - A^{15}N_{control} \quad (7.3)$$

where the control was the value measured in unlabelled samples (natural abundance).

The quantity of ^{15}N derived from the labelled litter deposited in autumn 2012 ($Q^{15}N$, in $\mu g\ ^{15}N\ g^{-1}$ sample) was computed as:

$$Q^{15}N = 10 \times E^{15}N \times N_{tot} \quad (7.4)$$

and the quantity of N derived from the labelled litter deposited in autumn 2012 in a sample (N litter-derived, N_{LD}, in $\mu g\ N\ g^{-1}$ sample) as:

$$N_{LD} = 100 \times \frac{Q^{15}N}{E^{15}N_{initial}} \quad (7.5)$$

where $E^{15}N_{initial}$ is the ^{15}N excess in the labelled litter deposited (in %).

Finally, we computed for each sampling date the proportion of N from the initial labelled litter which was recovered. For each layer sampled, the N recovery (N_{rec}, in % N deposited) was computed as:

$$N_{rec} = \frac{N_{LD} \times m}{10 \times N_{dep}} \quad (7.6)$$

where m is the mass of the sample (in $g\ m^{-2}$) and N_{dep} is the amount of N deposited with the labelled litter in autumn 2012 (in $mg\ N\ m^{-2}$). The N recovery was computed using mean isotopic compositions of the layers at the given sampling dates and overall averaged or estimated masses. We only measured the mass of the two first soil layers in forests. The mass of the samples from deeper horizons was estimated (m_{est}, in g) using soil density (D):

$$m_{est} = S \times T \times D \quad (7.7)$$

where S is the surface area of sampling and T is the thickness of the soil layer (in cm). In SW Siberian aspen forests, big tree roots are numerous in the soil surface and

their volume cannot be neglected when estimating the mass of soil. For 0 to −5 cm, we compared these measurements (m_{meas}) with m_{est}. Mass estimations with soil density conducted to over-estimations by a factor 1.85–2.96, probably because of the volume of coarse roots. Assuming the over-estimation would be similar among the first 15 cm of the soil, we corrected m_{est} dividing it by the mean over-estimation factor of the site.

All data handling and statistics were performed with R version 3.2.2 (R Core Team 2015).

7.2.8 Measurement of litter decay in litterbags

Because of the intermingling of decomposing leaves in the experimental plots, it was not possible to distinguish precisely the remaining ^{15}N-labelled litter on the area from which litter samples were collected. In autumn 2013, a litterbag experiment was set up to better characterize the contrasting litter decay patterns between our sites. We deposited on each site, and for each vegetation cover, 30 litterbags randomly distributed on the border of the ^{15}N experimental plots. Each litterbag consisted of a 150 cm^2 envelope made with a nylon net with a mesh size of 1.5 mm (Staaf 1980), allowing the penetration of meso-fauna and part of the macro-fauna. Each litterbag contained 2 g of air dried litter collected from the same site (Chebula) under the same conditions where the ^{15}N-labelled litter was produced. The litterbags were deposited on the soil surface after removing the fresh litter and fixed with a nail.

At each subsequent sampling date, we collected five of these litterbags, each from a different experimental plot. The remaining litter was carefully removed from the litterbag and dried at 60 °C to constant weight. Soil particles were removed by hand during the first year of litter decomposition. Later, the ash content was measured in all litterbags and sample weight was corrected by taking into account the contamination of the litterbags with soil particles.

7.3 Results

7.3.1 Temperature monitoring

Over the period of monitoring (autumn 2013–autumn 2015), the soil temperatures at −5 and −15 cm followed the variations of air temperature, except in winter where air and soil temperatures were decoupled (Fig. 7.1). The amplitude of temperature variation was lower in soil than in the air and slightly lower at −15 than at −5 cm.

Except during wintertime, soil temperature was generally higher at BAR and SAE than at SAW and TOM. While air temperature was almost the same in the two

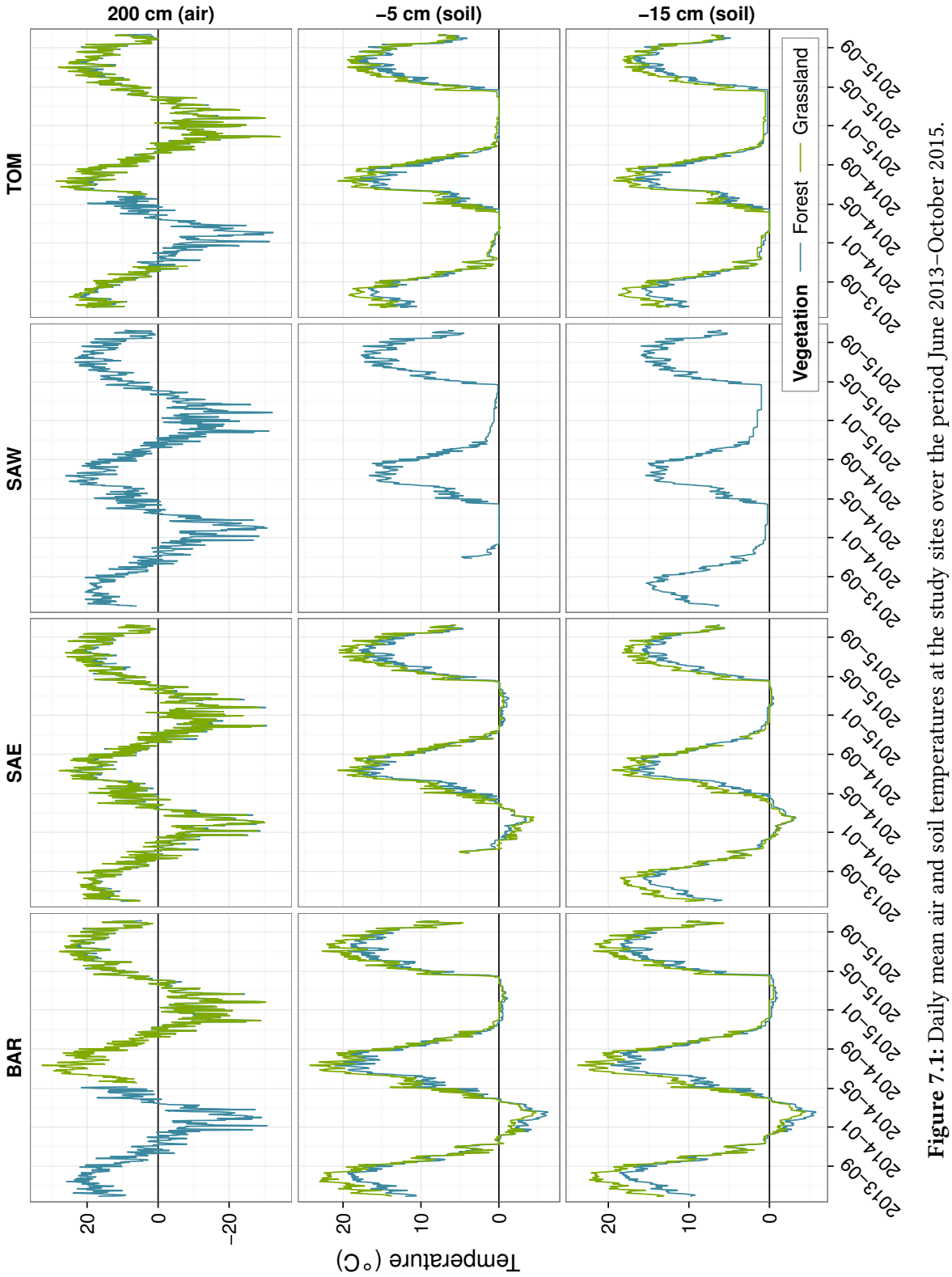


Figure 7.1: Daily mean air and soil temperatures at the study sites over the period June 2013–October 2015.

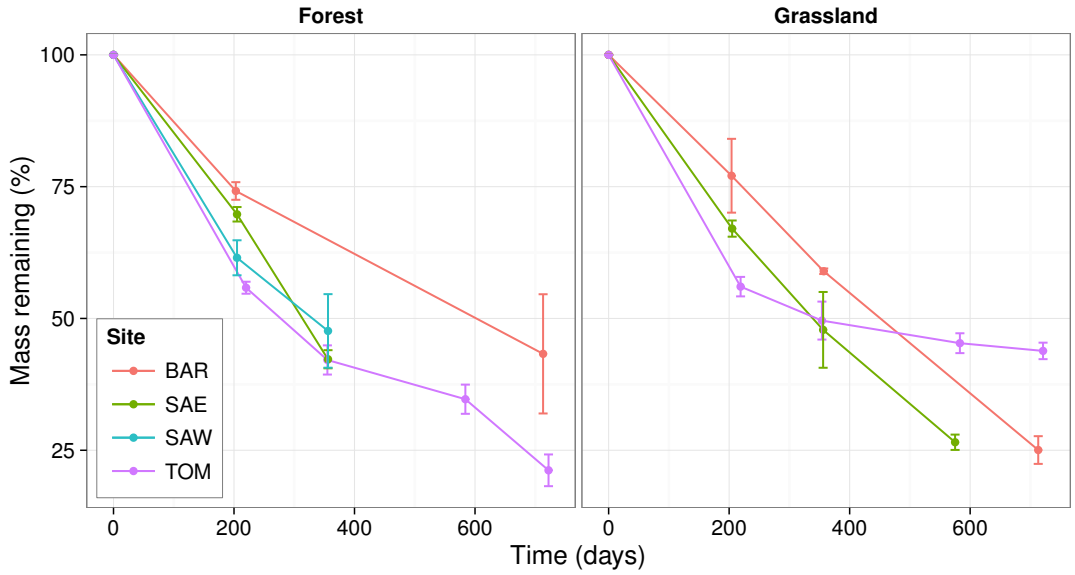


Figure 7.2: Rates and kinetics of decomposition in the litterbags deposited in autumn 2013. Mean and standard error of the mean (n = 2–5).

vegetation covers, soil temperature tended to be higher under grassland than under forest, particularly in summer.

In winter, the decoupling between air and soil temperatures was the result of the presence of a seasonally permanent snow-pack (Chap. 4). The soil was frozen at −5 and −15 cm at BAR and SAE but not at SAW and TOM. Also, at BAR and SAE, temperature was lower under grassland than under forest. This was related to the snow-pack, which was thicker at SAW and TOM than at BAR and SAE and thicker in forests than in grasslands (Table 7.1). Particularly at BAR and SAE, soil temperature tended to be lower during the winter 2013–2014 than during the winter 2014–2015. This is because the snow-pack was shallower (Table 7.1) and the snow season began later, so the soil was already frozen, in the winter 2013–2014 than in the winter 2014–2015.

7.3.2 Kinetics of litter decay

In both forest and grassland, the mass loss of litter in the litterbags was faster at TOM and SAW than at SAE and BAR in the first year of decomposition (Fig. 7.2). In spring 2014 (first date of sampling for the litterbags), 26–40 % of the mass was lost in forest and 23–44 % in grassland. In autumn 2015 (the last sampling to date), it was 57–79 % and 57–75 %, respectively.

In grassland, while the mass loss continued with the same trend over time at SAE and BAR, it decelerated at TOM in 2014. As such, in autumn 2015, the remaining

mass of litter in grassland was higher at TOM (43 %) than in the other sites (25 % at BAR).

7.3.3 Total N in soil samples

All topsoil profiles presented decreasing N concentrations with depth (Fig. 7.3). This trend was not impacted by sampling date but we observed some discrepancies, particularly at SAE forest. On average, we observed higher spatial (as indicated by standard errors) and time (as indicated by the difference between sampling dates) variabilities at SAE than in the other sites. The reasons for such patterns are discussed below.

7.3.4 ^{15}N signal in the layers sampled

We were able to distinguish the remaining ^{15}N-labelled litter deposited in autumn 2012 only at the first date of sampling (spring 2013). At this date, all the samples of remaining ^{15}N litter had a δ^{15}N lower than the initial litter (Tables 7.3 and 7.4).

Alive herbaceous vegetation was not always sampled in forests because the dates of our samplings do not really fit with the phenology of the understorey vegetation. The samplings occurred either too early in spring or too late in autumn. In forest, from the first sampling date (i.e. spring 2013) at SAE and from spring 2014 at SAW, the results available suggest that the understorey vegetation was enriched in ^{15}N (Table 7.4). In grassland, we observed a strong enrichment of the vegetation in ^{15}N in spring 2013 (155–283 ‰) and lower ones at the subsequent dates. The highest enrichment was observed at BAR.

The litter collected above the protection net, resulted from wind-blown material and/or from the vegetation growing in the seasons subsequent to deposition. Particularly in forest, the origin of such material (litter above net) can be diverse so the results have to be considered with care. There was no consistent trend over time in the enrichment of the litter above net in forests (Table 7.4). In fact, the enrichment was irregular with time at BAR and SAW, increasing at SAE and decreasing at TOM. In grasslands, due to the height and the density of grasses and because they mostly remain encroached into the soil when dead, the origin of the litter collected above the net is less uncertain. All the litters collected above the net in grasslands were clearly enriched in ^{15}N (Table 7.4). However, with the few sampling dates analysed until now, it is difficult to infer patterns in temporal dynamics of such enrichment.

The signal was lower in the litters collected below the net (Table 7.4) than in the labelled material (Table 7.3). Below the net protecting the ^{15}N-labelled litter is a mix between the ^{15}N-labelled litter, older material and eventually fractions of decomposing younger litter. Such dilution of the labelled litter is likely to increase

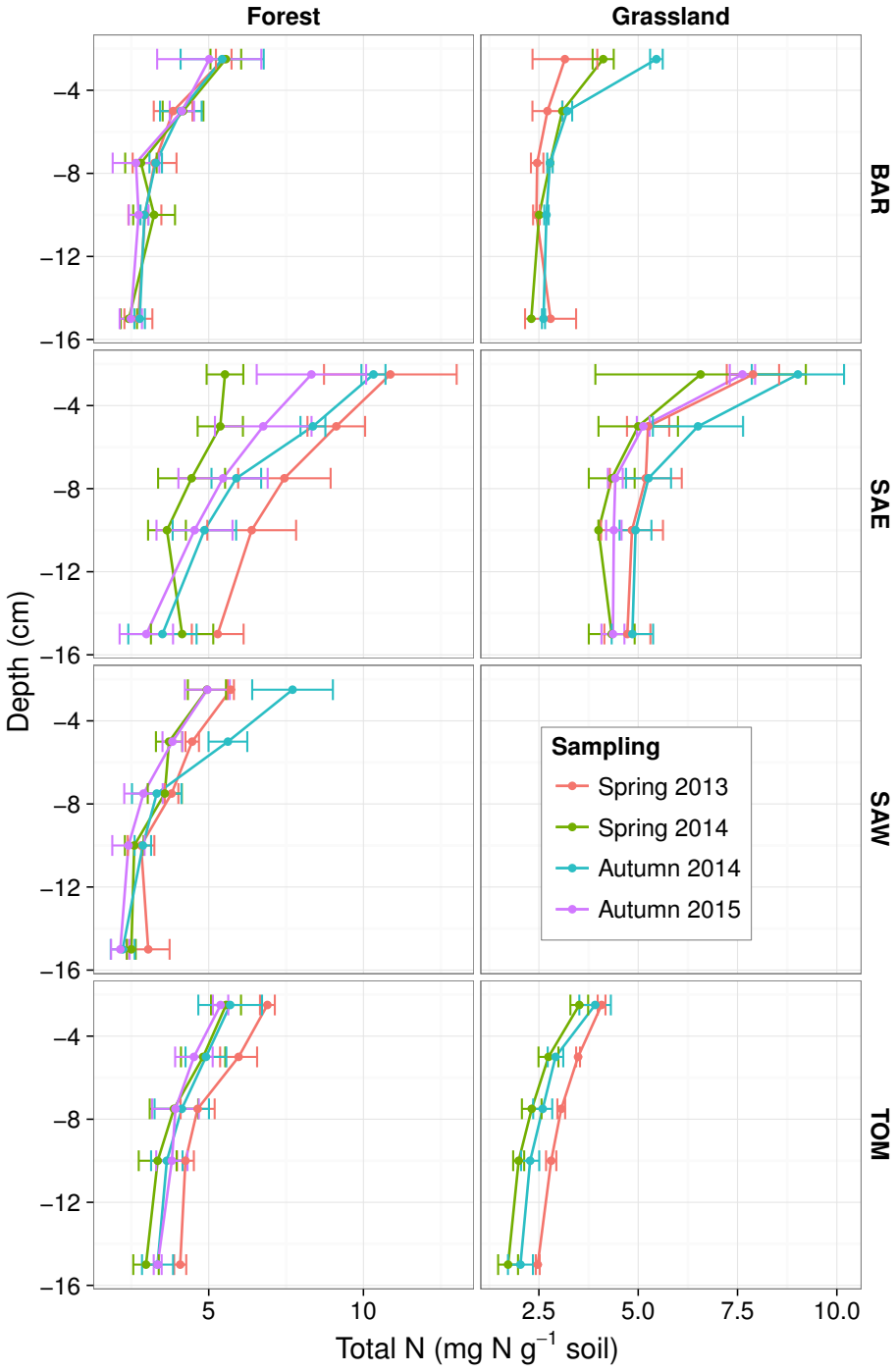


Figure 7.3: Profiles of total N concentrations in the soil layers for the different samplings. Mean and standard deviation (n = 1–6).

over time. In all forests and grasslands, the litter collected below the net was clearly enriched in ^{15}N at all the samplings for which the analyses are available (Table 7.4).

In forest, BAR, SAW and TOM presented an enrichment of all the soil layers from the first sampling, in spring 2013 (Fig. 7.4). At SAE forest, the enrichment of the three upper soil layers was clearly observed from autumn 2014. In fact, no enrichment was measured in spring 2013 and the values obtained for spring 2014 were close, or lower than the control (natural abundance). In the four forest sites, soil enrichment tended to increase in the upper layers until autumn 2015. The average $\delta^{15}N$ values of autumn 2015 in the upper layers were generally lower than those of autumn 2014 and even of those of spring 2014 at BAR and SAW. On average, the ^{15}N enrichment of the upper soil layers was greater at SAW and TOM than at BAR and SAE.

In grassland, ^{15}N enrichment did not occur as deep as in forest for the three sites (Fig. 7.4). At BAR grassland, ^{15}N enrichment concerned almost exclusively the two first soil layers. It was observed from spring 2013 and increased over time (to date, analyses for autumn 2015 are not available). At SAE grassland, enrichment was only observed in the first soil layer in spring 2013, it increased over time both in intensity and depth (until 7.5 cm). At TOM grassland, no enrichment was measured in the 10–15 cm soil layer but all the layers above were enriched in ^{15}N from the first date of sampling.

7.3.5 N recovery over time

Along with the decomposition of the labelled litter, its N was distributed among different ecosystem compartments (Fig. 7.5).

At the first date of sampling, nine months after deposition, a substantial part of the deposited N remained in the residues of the labelled litter deposited (Fig. 7.5). In forest, these residues contained 86 and 35 % of the deposited N at SAW and TOM, respectively. At BAR and SAE forests, the residues of the labelled litter virtually contained more than 100 % of the N deposited. As we will discuss, these values are probably due to over-estimations of masses. Nevertheless, the proportion of N that was present in the litter below the protection net decreased with time and this decrease was stronger and faster at SAW and TOM than at BAR and SAE forests. In grassland, similar trends were observed: high proportions, > 50 %, of N were recovered in the litter layers below the net at the first date, these proportions were decreasing over time and the decrease was faster at TOM than at BAR and SAE.

From the first sampling date, in forest, 15 (SAE) to 43 % (TOM) of the deposited N was found in the top 15 cm of the soil (Fig. 7.5). A consequent transfer of N from the litter to the soil was rather immediate at TOM while it took longer in the other sites. Due to the restricted number of samples and to relatively high uncertainties in both the estimation of mass and isotopic composition, we can hardly compare the sampling dates for a given layer. Nevertheless, there was a trend for increasing

Table 7.4: Isotopic composition of the vegetation and litter layers sampled. Mean δ^{15}N (‰) and standard deviation of *n* samples. The analyses of the samples taken in autumn 2015 are ongoing. The δ^{15}N of the deposited litter was 528 ‰ in forest and 3159 ‰ in grassland.

	Nat.	Spring 2013			Spring 2014			Autumn 2014		
	Ab.	*n*	mean	sd	*n*	mean	sd	*n*	mean	sd
BAR forest										
Vegetation	·	·	·	·	·	·	·	·	·	·
Litter above	2.87	3	25.68	3.11	3	6.40	3.50	2	17.37	13.22
15N litter	·	3	221.19	74.33	·	·	·	·	·	·
Litter below	2.03	3	4.71	0.96	2	36.71	7.59	3	30.35	7.77
SAE forest										
Vegetation	0.37	6	5.19	3.95	6	8.62	2.38	2	15.74	4.68
Litter above	1.09	3	7.96	11.39	6	8.24	4.41	3	16.65	3.97
15N litter	·	3	410.01	55.46	·	·	·	·	·	·
Litter Of	1.63	3	8.89	6.06	6	42.54	19.38	3	31.99	11.52
Litter Oh	1.63	2	3.27	0.03	·	·	·	·	·	·
SAW forest										
Vegetation	2.04	3	3.90	2.38	3	7.77	0.81	2	5.20	1.07
Litter above	1.51	3	39.61	13.64	3	8.46	1.78	2	13.78	1.51
15N litter	·	3	210.85	65.81	·	·	·	·	·	·
Litter below	2.54	3	13.15	11.97	3	36.15	12.21	3	23.16	6.75
TOM forest										
Vegetation	·	·	·	·	·	·	·	·	·	·
Litter above	3.79	3	72.94	61.90	3	15.58	5.07	3	9.08	6.91
15N litter	·	3	321.47	180.27	·	·	·	·	·	·
Litter below	4.11	3	57.66	36.31	3	41.18	14.56	2	26.16	12.25
BAR grassland										
Vegetation	3.01	6	282.65	211.70	3	73.10	41.25	3	68.44	21.34
Litter above	3.01	·	·	·	3	135.78	74.42	3	91.73	30.25
15N litter	·	3	1667.20	567.91	·	·	·	·	·	·
Litter below	0.55	3	154.78	69.60	3	494.76	177.78	3	231.35	45.44
SAE grassland										
Vegetation	2.54	6	155.37	60.93	6	76.06	16.07	2	30.91	22.98
Litter above	2.54	·	·	·	6	83.66	46.22	3	132.31	4.64
15N litter	·	3	1633.85	268.88	·	·	·	·	·	·
Litter below	·	3	389.37	130.56	6	283.79	83.91	3	405.30	118.64
TOM grassland										
Vegetation	5.33	6	214.13	149.45	3	115.52	61.57	·	·	·
Litter above	5.33	·	·	·	3	245.34	63.76	·	·	·
15N litter	·	3	2069.96	134.14	·	·	·	·	·	·
Litter below	3.34	3	683.33	216.86	3	759.80	102.62	·	·	·

Nat. Ab.: Natural abundance · : not available

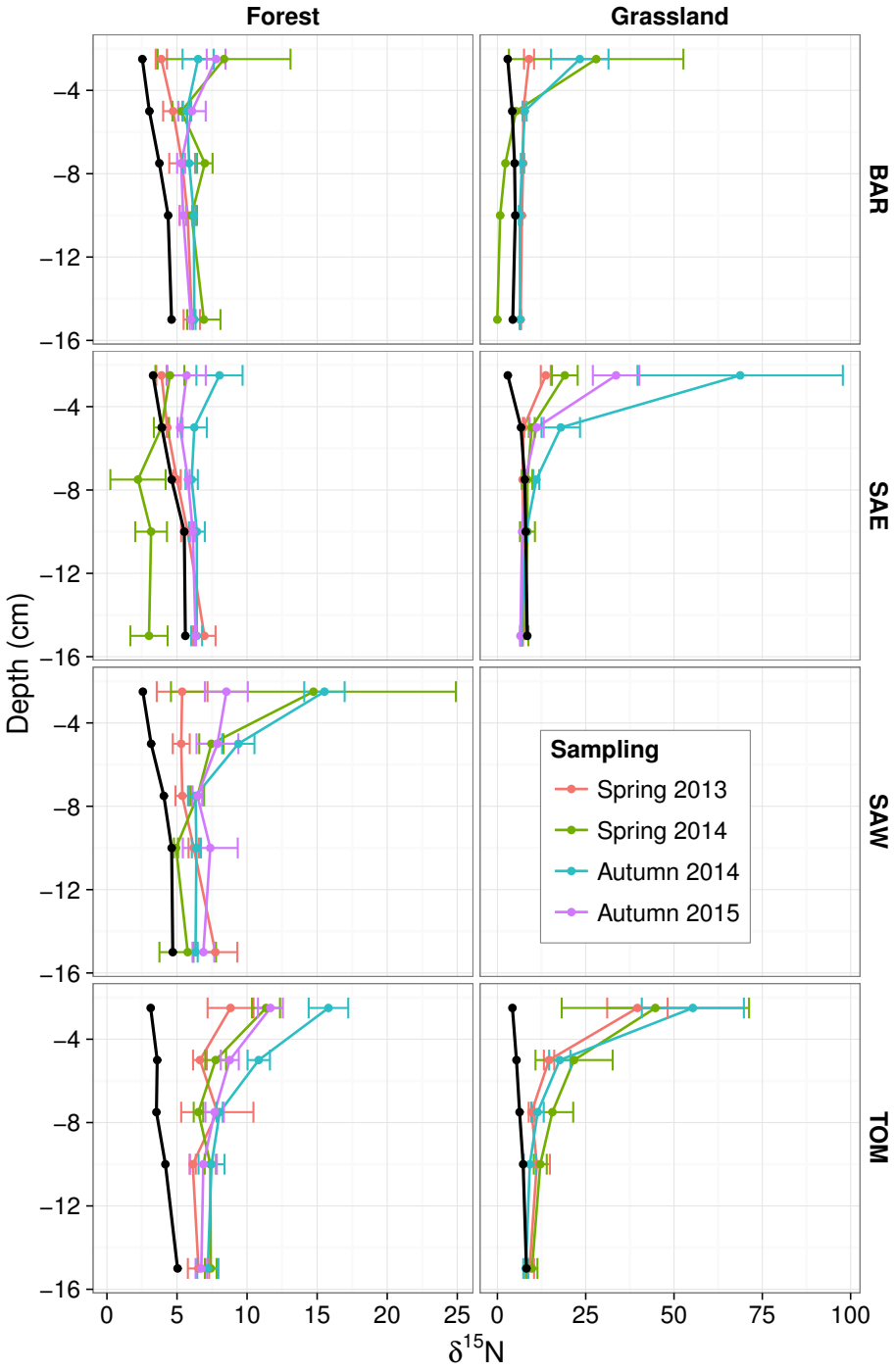


Figure 7.4: Profiles of δ^{15}N (‰) in the soil layers for the different samplings. Natural abundances are displayed in black. Mean and standard deviation (n = 1–6). The δ^{15}N of the deposited litter was 528 ‰ in forest and 3159 ‰ in grassland.

stocks of N derived from the litter of 2012 in the soil until autumn 2014. In autumn 2015, the N recovered in the soil layers was lower than a year before in all sites. In all sites, the upper soil layer contained most of the N transferred to the soil from the litter. With time, the second layer tended to concentrate increasing amounts of this N.

In grasslands, similar dynamics were observed but the transfer of N to the first soil layer was greater than in forests (Fig. 7.5). N transfers to the deeper soil layers were very low and concerned essentially the second layer. Again, the transfer was immediate, but after this fast transfer, the stocks increased slowly at TOM. On the contrary, the transfer was delayed and regularly increasing at BAR and SAE.

7.4 Discussion

7.4.1 Critical analysis

At our study sites, soil ^{15}N enrichment generally increased until autumn 2014 from which it started to decrease (Fig. 7.4). A similar trend was reported in several experiments following ^{15}N issued from the decomposition of labelled organic material deposited on the soil surface: for example beech leaf-litter in western Europe (Zeller et al. 2001, 2000), eucalyptus harvest residues in Congo (Versini et al. 2013) or pine harvest residues in Australia (Blumfield et al. 2004). However, we note that the trend of ^{15}N enrichment in the soil layers with time may not be perfectly detected in our experiment. Coupled with other technical issues, this has likely altered the precision of our N budgets (Fig. 7.5). First, the labelling of initial material was rather low, particularly in forest (Table 7.4). As a comparison, Zeller et al. (2001) used a beech leaf litter with 3.24 atom % ^{15}N abundance. A low labelling necessitates high precision both in sampling and isotopic analyses. Slight variations in the precision of either of these two steps may produce noise in the signal and alter the results when computing mean on a few replicates.

The total N concentrations in the soil layers sampled (Fig. 7.3) can be used as a proxy for sampling precision. In fact, there is no reason—unless a truly high spatial heterogeneity in litter accumulation and/or soil properties at the plot level or important seasonal variations, for example as the result of soil freezing or moisture content—for a strong variation in the total N soil profile between the sampling dates. The relatively high variations observed at SAE, particularly in forest, may indicate the samplings were not always regular at this site. It is probable that the criteria differentiating the different litter layers (Of, Ol and Oh according to the fragmentation level) were not always perceived the same way between different sampling dates and different operators. As such, 1–2 cm difference in the sampling of litter may induce a vertical translation of the soil layers. For example, it

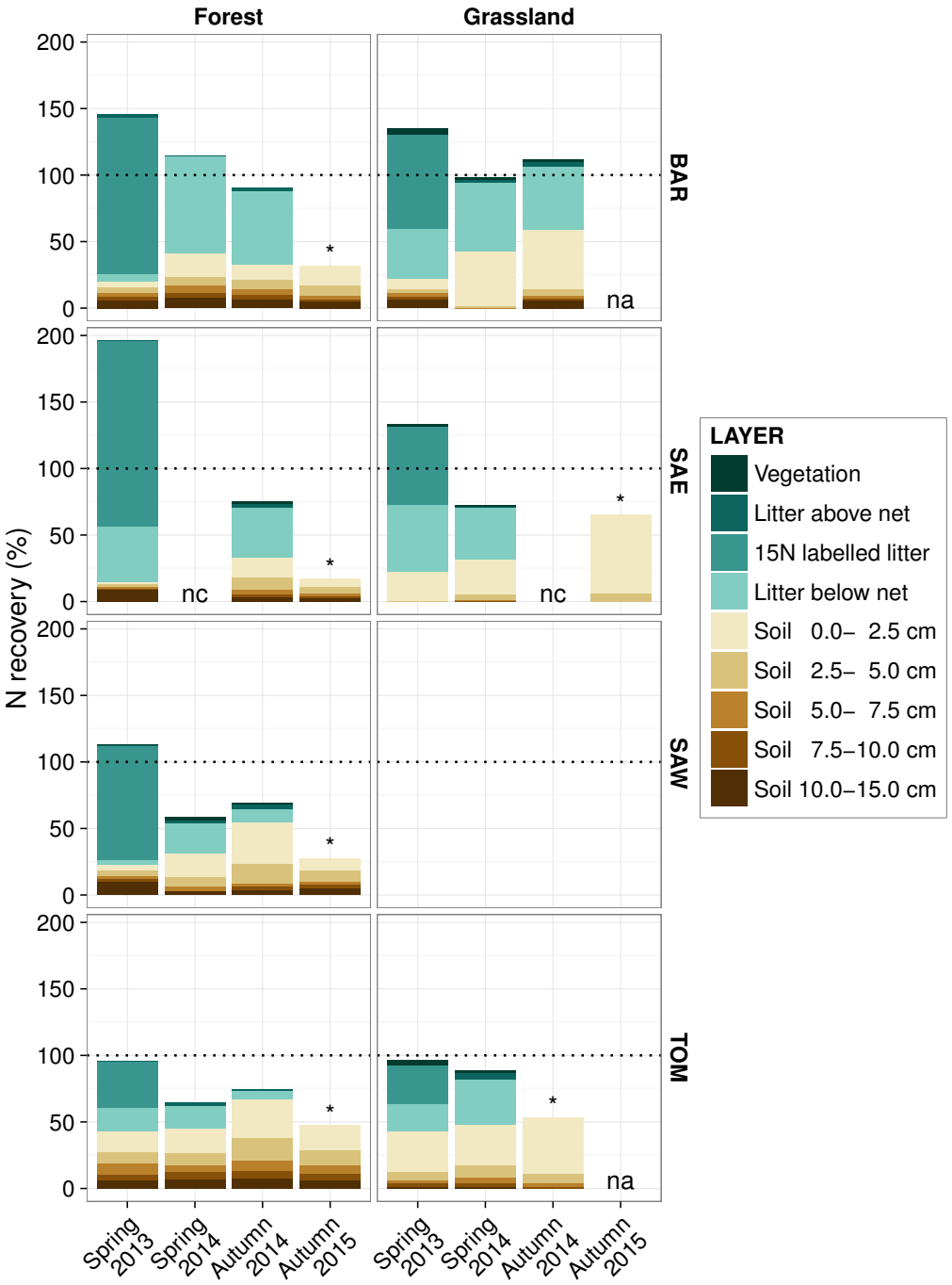


Figure 7.5: Recovery of N from the labelled litter deposited in autumn 2012 within the different layers sampled and over the study period. "na" stands for "not available" (mainly ongoing analyses), "nc" for "not computed" (major discrepancies in the ^{15}N recovery) and "*" indicates that vegetation and litter analyses are still ongoing.

is possible that, in spring 2013, mineral soil was sampled about 2 cm deeper than in the other dates. Anyway, discrepancies between operators and sampling dates are inherent of such experiments and we took many precautions to limit their effect. Also, some discrepancies were observed in the analyses of controls (natural abundances) between two runs of analyses and between two laboratories. In the current stage, we estimate the analytical precision of our isotopic analyses at about 1 ‰, which is rather high considering that the mean enrichment in ^{15}N in the deepest soil layers was of the same order of magnitude. We are currently working with the engineers and technicians of the analytical platform to improve the precision of our measurements (the objective is to reach about 0.3 ‰). Subsequent analyses may refine our results.

Finally, the measurement and the estimation of the mass of the soil samples was a bit tricky in our study sites. In fact, the dense net of big roots, coupled with the small surface area of sampling (we had to preserve labelled area for subsequent samplings), often impeded to properly sample all the soil material. As a consequence, the amount of sampled material was very variable for a given volume. Thus, we did not sampled all the volume we planned below 5 cm and we estimated masses with soil densities and a factor of correction (see materials and methods). Therefore, the quality of the N recovery might have been altered, partly explaining why we are not able to clearly distinguish temporal dynamics in soil (Fig. 7.5). It is also possible that the mass of the remaining labelled-litter sampled at the first date was over-estimated, and the ^{15}N signal over-diluted, at BAR and SAE because of mixing with unlabelled fragments, explaining the N recovery > 100 % in spring 2013.

Incomplete N recoveries (Fig. 7.5) might result from several phenomena. Firstly, we did not analyse the isotopic composition of all the ecosystem compartments susceptible to contain N derived from the deposited litter. Notably, tree organs like roots, stem and branches are likely to contain substantial amounts of ^{15}N (Blumfield et al. 2004; Versini et al. 2013; Zeller et al. 2001, 2000). Secondly, litter fragments, dissolved organic N or N ions may have been exported deeper than 15 cm, particularly in forests where we measured soil enrichment only to this depth. Soil fauna and fungi can also be responsible for lateral transfers of N, out of the experimental plots (Caner et al. 2004).

7.4.2 Site or vegetation cover specific patterns in N dynamics

Contrasting situations

Difference between vegetation cover On the scale of one site, i.e. between aspen forest and grassland, the major difference was the depth of N transfer into the soil which was deeper in forest than in grassland. In a general manner, the N derived from litter was retained in the first centimetres of the mineral soil in grassland while

it was transferred deeper in forest.

This has certainly to be related to different plant–soil interactions and different vegetation cover phenology. As fine root exploration is denser in grassland topsoil than in forest topsoil, we suppose that an efficient uptake of N by grasses in the first soil layers limits N migration down the profile. It is also possible that grasses are active earlier in the season than trees and understorey species, when there is a stronger potential of drainage because the soil is saturated by melt-water.

In addition, soil organic matter from grasslands was found to be inherently more productive of ammonium (NH_4^+) than SOM from wooded sites (Booth et al. 2005) and ammonium is known to be less mobile in soil than nitrate (NO_3^-) (Orcutt and Nilsen 2000; Tinker and Nye 2000). Also, the uptake efficiency of NH_4^+ for both plants and micro-organisms is far superior to those of NO_3^- and amino acids (Kuzyakov and Xu 2013). This may partly explain the apparently efficient N immobilization in the very topsoil in grasslands of SW Siberia, impeding the transfer towards deep soil layers.

Difference between sites Our results revealed contrasting situations between sites and between the two vegetation covers. Focussing on the differences between our study sites, it is possible to detect two groups with contrasting N dynamics. These broad dynamics are similar in aspen forest and grassland for a given site. These two groups fit with the bioclimatic zones forest-steppe (BAR and SAE) and sub-taiga (TOM and SAW) and we further refer to them as such.

Litter decays in our litterbag experiment were consistent with the field observation that litter generally does not accumulate in sub-taiga (e.g. SAW and TOM) while it does in forest-steppe (e.g. BAR and SAE). We observed mass loss all over the year, in particular during wintertime and summertime (Fig. 7.2). However, since our samplings occurred only twice a year, in mid-spring and mid-autumn, we do not know whether there is a continuous rate of mass loss (e.g. over winter) or whether it occurs more intensively at key periods (e.g. snow-melt, summer rain-events).

At TOM grassland, we observed a sharp decrease in the decomposition rate in litterbags after one year (Fig. 7.2). Such a phenomenon may correspond to a second phase of decomposition, where the mass loss is very slow. It has been referred to as the "maximum decomposition limit" and has been reported notably in Scandinavia (Berg et al. 1996, 2009) and Canada (Trofymow et al. 2002). However, it usually occurs in suboptimal conditions (e.g. cold northern forests; Harmon et al. 2009) and at more advanced stages of decomposition (once 70–80 % of the initial mass has been lost). This result would be partly in contradiction with the inferences on climatic conditions we made above. Also, it would occur at a surprisingly low mass loss proportion (about 50 %). To date, our litterbags mass loss measurements have not been corrected for potential soil contamination. We plan to determine ash content

in order to improve the precision of our measurements. If the trends are confirmed, they would indicate that other factors, additional to climate and possibly varying on the scale of the site, may exert substantial controls on litter decomposition.

In this study, we found that leaf-litter decomposition and N transfer to soil were slower in forest-steppe than in sub-taiga. In sub-taiga, the transfer of N occurred deeper, the total amount of N which was transferred was higher, as well as the amount of litter-derived N which was stored in the soil.

Potential mechanisms driving the differences between sites

Biochemistry of the litter Several abiotic and biotic factors can be responsible for the different rates of litter decay observed in the first two years of decomposition at our field sites. Plant traits and litter quality (i.e. chemical composition) were found to explain a great part of the differing rates of decay observed in inter-site comparisons (Cornwell et al. 2008; Zhang et al. 2008). However, in our study all litterbags contained the same litter, thus differing decays were not the result of litter quality itself, except for the differences between forest and grassland. Together with the relative homogeneity of the C and N contents of the aspen forest leaf litterfalls (Table E.2)—but also in other nutrients such as P, K, Ca and Mg (data not shown)—this result suggest that other factors may explain the different litter decays between our field sites, both in litterbags and in natural conditions, at least for aspen leaf litter in forest.

Also, tree leaf litter is not the only constituent of forest floors. Other types of material (e.g. tree branches, understorey vegetation), mixed with leaf material, are likely to modulate the overall decomposition processes in forest floors. It would be interesting to evaluate the role of the understorey vegetation community composition—diversity, functional traits—(Hättenschwiler et al. 2005).

Climate Climate is a seducing candidate for explaining the decay patterns we observed, notably because of contrasting winter and summer conditions between our field sites. Climate impacts litter decomposition either directly or indirectly. Litter fragmentation can result from light, wind, precipitation or freezing, which are climate variables, but also from animal and plant activity, which themselves depend on climatic conditions (Berg and McClaugherty 2014; García-Palacios et al. 2013; Wall et al. 2008). Climate also controls decomposers (e.g. micro-organisms) and extracellular enzyme activities through moisture and temperature conditions (Buée et al. 2005; Wallenstein et al. 2009). In SW Siberia, it is possible that winter temperature at the soil surface and summer moisture conditions largely control the early stages of litter decomposition. In fact, the generally thick snow-pack in sub-taiga insulates soil from freezing at wintertime while a thinner snow-pack in forest-steppe does not always avoid soil freezing (see our monitoring over 2013–2015, Fig. 7.1). Despite

being under the threshold of 10 °C, under which litter decomposition is often very low (Zhang et al. 2008), the difference in temperature and water availability between frozen and unfrozen litters may allow the latter to continue decomposing during winter. In fact, microbial activity continues over-winter, as it was reported in several and diverse snow-covered environments (Brooks et al. 1996; Groffman et al. 2006; Grogan and Jonasson 2005; Mast et al. 1998; Monson et al. 2006a; Wallenstein et al. 2009; Wang et al. 2010). The height of the snow-pack modulates microbial activity, as shown by lower respiration rates under shallower snow-cover and colder soil (Monson et al. 2006b). In addition, in SW Siberia, over the rest of the season and particularly in summer, soil and soil floor are much drier in forest-steppe than in sub-taiga (Chap. 4). Overall, it seems that climatic conditions of sub-taiga favours litter decomposition over the year, while seasonal conditions may reduce it drastically in forest-steppe.

This hypothesis fits with field observations of forest and grassland floors. For example, summer observations reveal that almost all non-structural parts (e.g. ex-photosynthetic tissues) of the leaf litter have disappeared in sub-taiga (TOM and SAW). Only structural parts of leaves, mixed with branches, remain in a thin and not continuous layer on the top of the mineral soil. On the contrary, in forest-steppe and particularly under forested vegetation cover, it is possible to distinguish several litter layers with different levels of fragmentation and containing non-structural parts.

In addition, depending on the water saturation of the soil profile, precipitation induces drainage and thus potentially the leaching of solubles and the movement of particles downwards. Studies in deciduous and coniferous forests have reported higher ecosystem N retention and lower exports in years with deep snow cover (Brooks et al. 1998; Lewis and Grant 1980; Mitchell et al. 1996; Peters and Leavesley 1995). Studies in diverse forest and tundra ecosystems reported that increased snow cover allowed higher levels of microbial N immobilization (Brooks and Williams 1999; Buckeridge and Grogan 2010), while shallower snow-packs were associated with higher N export (Boutin and Robitaille 1995; Brooks and Williams 1999; Brooks et al. 1996; Callesen et al. 2007; Fitzhugh et al. 2003; Groffman et al. 2006; Groffman et al. 2001; Lipson et al. 1999; Nielsen et al. 2001). On the scale of SW Siberia, higher microbial activity under the deeper snow-pack of sub-taiga may allow higher SOM processing and higher N immobilization. On the contrary, lower amounts of SOM would be processed during winter in forest-steppe and the lysis of microbial cells induced by freezing may lead to higher N exports by leaching at snow-melt. However, even if most of the yearly drainage is associated with snow-melt in SW Siberia, the levels of drainage in forest-steppe are probably rather low and are lower than those of sub-taiga (Chap. 4). In addition, soil freezing can affect fine roots or root-symbionts (Cleavitt et al. 2008; Kreyling et al. 2012; Repo et al. 2014; Tierney et al. 2001) and lead to reduced N uptake by trees (Campbell et al. 2014b) which could

potentially contribute to greater N export from forests (Brooks et al. 2011).

Finally, there is increasing evidence that the role of climate has often been overseen in litter decomposition studies (Bradford et al. 2015; Prescott 2010). If we are tempted to evacuate the role of litter quality in our study, the integration of other factors, such as soil properties and processes or local environmental conditions (e.g. micro-topography), is likely to improve our understanding of decomposition in the whole litter–soil organic matter continuum (Bradford et al. 2015; Prescott 2010).

Soil fauna Soil fauna exerts a significant control in regulating litter decomposition processes (Kampichler and Bruckner 2009; Osler and Sommerkorn 2007; Rouifed et al. 2010; Wall et al. 2008). Soil fauna, affect decomposition via fragmentation, gut processing, translocation of the litter material but also through the modification of the structure and activity of microbial communities (Hättenschwiler and Gasser 2005; Lavelle and Spain 2001; Wolters 2000). We cannot exclude that soil micro- and meso-fauna, but also microbial communities, are different in composition or in density between our field sites. Because of the small mesh size of the litterbags (1.5 mm), part of the meso- and all macro-fauna were excluded from the study of decay in litterbags (Bradford et al. 2002; St John 1980). However, these organisms may be involved in the whole litter decomposition process at the study sites and notably in those of the ^{15}N-labelled litter.

Soil properties While the soils have developed from a common parent material, differing climatic conditions induce different soil processes. The resulting contrasting soil types certainly affect N dynamics.

Our sub-taiga soils have higher fine-silt content than forest-steppe (Table 7.2). Fine-silts are involved in aggregate formation. Indeed, the size of micro-aggregates ranges from silt-size (Virto et al. 2008) to finer scales (Calabi-Floody et al. 2011; Chenu and Plante 2006; Dümig et al. 2012). Micro-aggregates constitute a physical barrier to micro-organisms and enzymes or inhibit their activity due to local anoxic conditions (Balesdent et al. 2000; Kemmitt et al. 2008). Turnover times of organic matter increase with decreasing particle size and the highest turnover times were observed in the fine-silt and the clay fractions (Balesdent 1996; Balesdent et al. 1998). In addition, the stability of aggregates is enhanced by iron (Fe) and aluminium (Al) oxides (Duiker et al. 2003). These oxides are also more abundant in our sub-taiga sites than in our forest-steppe sites (but SAE is the richest site in Al oxides; Table 7.2).

Cotrufo et al. (2015) suggested two pathways of SOM formation from the decomposition of litter. At the early stages of litter degradation, mostly non-structural compounds are lost and are incorporated into the microbial biomass at high rates, resulting in efficient SOM formation ("dissolved organic matter–microbial path"). Along with this phenomenon, and until the later stages of litter decomposition, the

physical transfer of litter fragments would contribute to the formation of coarse particulate SOM. These two pathways are likely to result in different mechanisms of SOM stabilization: organo–mineral association via the DOM–microbial path and inherent chemical recalcitrance via the physical-transfer path. Physical occlusion by incorporation of SOM in aggregates could occur in both pathways. On the long-term, the fate of the SOM issued by these pathways would depend on the stabilization potential and the climatic conditions of the soil (Cotrufo et al. 2015, 2013). In our sub-taiga sites, the faster rates of litter decomposition suggest that the DOM–microbial pathway of the applied labelled litter is more completely realised than in our forest-steppe sites.

Microbial products have a particularly high affinity for mineral surfaces (Kleber et al. 2007; Mikutta et al. 2009) and microbial processing is known to enhance SOM stabilization (Rawlins et al. 2007). Altogether these observations suggest that organic N stabilization would be more efficient in the soils of sub-taiga (TOM and SAW) than in the soils of forest-steppe (BAR, SAE).

Finally, depending on the competition for the N resource, variable forms of soluble N may dominate in the soil (Schimel and Bennett 2004). If there is a production of NH_4^+, it will interact strongly with negatively charged clay particles. By contrast, if NO_3^- is produced (the competition between plant and heterotroph being low enough to permit nitrifier to flourish), it will not interact with mineral surfaces and can be exported out of the system (Schimel and Bennett 2004).

7.5 Conclusion

The fate of ^{15}N derived from leaf-litter decomposition differed between forest and grassland. In a general manner, N was retained in the first centimetres of the mineral soil in grassland while it was transferred deeper in forest. Such a phenomenon has certainly to be related to different plant–soil interactions and vegetation cover phenology. As fine root exploration is denser in grassland topsoil than in forest topsoil, we suppose that an efficient uptake of N by grasses in the first soil layers limits N migration down the profile. It is also possible that grasses are active earlier in the season than trees and understorey species, when there is a stronger potential of drainage because snow-melt saturated the soil.

On the time scale of our study (three years), we observed, along with faster decay rates, faster releases of leaf litter-N in sub-taiga than in forest-steppe. As such, higher quantities of N were retrieved in the soil and the transfer was deeper in sub-taiga. Deeper transfer may be related to water dynamics. Notably, the drainage is more intense in sub-taiga because of higher snow levels and saturation of the soil water capacity. Interestingly, these higher drainage seem to not induce a too large loss of N from the system. As an explanation, we propose that the soils from

sub-taiga are efficient in retaining N. Such retention could result from soil physico-chemical properties (higher fine silt and oxides contents) enhancing soil organic matter stabilization, and/or by the immobilization of N in microbial metabolites. This hypothesis requires further investigations. In particular, it would be interesting to know in which form(s) N is released and retained in the soil. For example, we expect ammonium and microbial products to be more associated with clay mineral surfaces than plant N.

Our results contradict our initial hypothesis that the cycling in the plant–soil system is faster in sub-taiga than in forest-steppe. In fact, while the decomposition is faster in the organic layer, the soil properties may explain the retention of N in the organo–mineral layers. To better identify the processes involved in N dynamics at our sites, it would be interesting to identify the forms of the ^{15}N (plant residues, microbial metabolites, ammonium, nitrate, etc.). Pursuing the monitoring in the long-term (e.g. for a decade) will allow to gain further insights in the mechanisms of N sequestration (Hatton et al. 2012, 2015; Zeller and Dambrine 2011).

Acknowledgements

G. Bougrovskaia and A. Litvinov, in Novosibirsk, and C. Dubreil, C. Gehin, L. Gelhaye, M.-C. Maintenant and J. Michel, in Nancy, regularly helped processing (sorting, drying, sieving, packing, grinding, weighing) piles of ^{15}N samples. C. Bréchet and C. Hossann performed isotope analyses.

References

AFNOR (1999). Qualité des sols. In: *Recueil de normes*. Vol. 1.

Balesdent, J. (1996). The significance of organic separates to carbon dynamics and its modelling in some cultivated soils. *European Journal of Soil Science* 47.4, 485–493. DOI: 10.1111/j.1365-2389.1996.tb01848.x.

Balesdent, J., Besnard, E., Arrouays, D., and Chenu, C. (1998). *Plant and Soil* 201.1, 49–57. DOI: 10.1023/a:1004337314970.

Balesdent, J., Chenu, C., and Balabane, M. (2000). Relationship of soil organic matter dynamics to physical protection and tillage. *Soil and Tillage Research* 53.3-4, 215–230. DOI: 10.1016/s0167-1987(99)00107-5.

Berg, B., Johansson, M.-B., Ekbohm, G., McClaugherty, C., Rutigliano, F., and Santo, A. V. D. (1996). Maximum decomposition limits of forest litter types: a synthesis. *Canadian Journal of Botany* 74.5, 659–672. DOI: 10.1139/b96-084.

Berg, B., Johansson, M.-B., Nilsson, Å., Gundersen, P., and Norell, L. (2009). Sequestration of carbon in the humus layer of Swedish forests — direct measurements. *Canadian Journal of Forest Research* 39.5, 962–975. DOI: 10.1139/x09-022.

Berg, B. and McClaugherty, C. (2014). *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration.* Third Edition. Springer Science + Business Media. DOI: 10.1007/978-3-642-38821-7.

Bimüller, C., Naumann, P. S., Buegger, F., Dannenmann, M., Zeller, B., Lützow, M. von, and Kögel-Knabner, I. (2013). Rapid transfer of 15N from labeled beech leaf litter to functional soil organic matter fractions in a Rendzic Leptosol. *Soil Biology and Biochemistry* 58, 323–331. DOI: 10.1016/j.soilbio.2012.11.021.

Blumfield, T. J., Xu, Z., Mathers, N. J., and Saffigna, P. G. (2004). Decomposition of Nitrogen-15 Labeled Hoop Pine Harvest Residues in Subtropical Australia. *Soil Science Society of America Journal* 68.5, 1751. DOI: 10.2136/sssaj2004.1751.

Booth, M. S., Stark, J. M., and Rastetter, E. (2005). Controls on nitrogen cycling in terrestrial ecosystems: A synthetic analysis of litterature data. *Ecological Monographs* 75.2, 139–157. DOI: 10.1890/04-0988.

Boutin, R. and Robitaille, G. (1995). Increased soil nitrate losses under mature sugar maple trees affected by experimentally induced deep frost. *Canadian Journal of Forest Research* 25.4, 588–602. DOI: 10.1139/x95-066.

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., and Wood, S. A. (2015). Understanding the dominant controls on litter decomposition. *Journal of Ecology* 104.1, 229–238. DOI: 10.1111/1365-2745.12507.

Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H., and Newington, J. E. (2002). Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99.2, 317–323. DOI: 10.1034/j.1600-0706.2002.990212.x.

Brooks, P. D., Grogan, P., Templer, P. H., Groffman, P., Öquist, M. G., and Schimel, J. (2011). Carbon and nitrogen cycling in snow-covered environments. *Geography Compass* 5.9, 682–699. DOI: 10.1111/j.1749-8198.2011.00420.x.

Brooks, P. D. and Williams, M. W. (1999). Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrological Processes* 13.14–15, 2177–2190. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2177::AID-HYP850>3.0.CO;2-V.

Brooks, P. D., Williams, M. W., and Schmidt, S. K. (1996). Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* 32.2, 93–113. DOI: 10.1007/bf00000354.

Brooks, P., Williams, M., and Schmidt, S. (1998). Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry* 43 (1), 1–15. DOI: 10.1023/A:1005947511910.

Buckeridge, K. M. and Grogan, P. (2010). Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. *Biogeochemistry* 101.1-3, 105–121. DOI: 10.1007/s10533-010-9426-5.

Buée, M., Vairelles, D., and Garbaye, J. (2005). Year-round monitoring of diversity and potential metabolic activity of the ectomycorrhizal community in a beech (Fagus silvatica) forest subjected to two thinning regimes. *Mycorrhiza* 15.4, 235–245. DOI: 10.1007/s00572-004-0313-6.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Korshunova, N. N. (2011). Changes in snow cover characteristics over Northern Eurasia since 1966. *Environmental Research Letters* 6.4, 045204. DOI: 10.1088/1748-9326/6/4/045204.

Bulygina, O. N., Groisman, P. Y., Razuvaev, V. N., and Radionov, V. F. (2010). Snow cover basal ice layer changes over Northern Eurasia since 1966. *Environmental Research Letters* 5.1, 015004. DOI: 10.1088/1748-9326/5/1/015004.

Bulygina, O. N., Razuvaev, V. N., and Korshunova, N. N. (2009). Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters* 4.4, 045026. DOI: 10.1088/1748-9326/4/4/045026.

Calabi-Floody, M., Bendall, J. S., Jara, A. A., Welland, M. E., Theng, B. K., Rumpel, C., and Luz Mora, M. de la (2011). Nanoclays from an Andisol: Extraction, properties and carbon stabilization. *Geoderma* 161.3-4, 159–167. DOI: 10.1016/j.geoderma.2010.12.013.

Callesen, I., Borken, W., Kalbitz, K., and Matzner, E. (2007). Long-term development of nitrogen fluxes in a coniferous ecosystem: Does soil freezing trigger nitrate leaching? *Journal of Plant Nutrition and Soil Science* 170.2, 189–196. DOI: 10.1002/jpln.200622034.

Campbell, J. L., Reinmann, A. B., and Templer, P. H. (2014a). Soil Freezing Effects on Sources of Nitrogen and Carbon Leached During Snowmelt. *Soil Science Society of America Journal* 78.1, 297. DOI: 10.2136/sssaj2013.06.0218.

Campbell, J. L., Socci, A. M., and Templer, P. H. (2014b). Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest. *Global Change Biology* 20.8, 2663–2673. DOI: 10.1111/gcb.12532.

Caner, L., Zeller, B., Dambrine, E., Ponge, J., Chauvat, M., and Llanque, C. (2004). Origin of the nitrogen assimilated by soil fauna living in decomposing beech litter. *Soil Biology and Biochemistry* 36.11, 1861–1872. DOI: 10.1016/j.soilbio.2004.05.007.

Chenu, C. and Plante, A. F. (2006). Clay-sized organo-mineral complexes in a cultivation chronosequence: revisiting the concept of the 'primary organo-mineral complex'. *European Journal of Soil Science* 57.4, 596–607. DOI: 10.1111/j.1365-2389.2006.00834.x.

Chlachula, J. (2003). The Siberian loess record and its significance for reconstruction of Pleistocene climate change in north-central Asia. *Quaternary Science Reviews* 22.18-19, 1879–1906. DOI: 10.1016/s0277-3791(03)00182-3.

Cleavitt, N. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Henry, K. S., and Driscoll, C. T. (2008). Effects of soil freezing on fine roots in a northern hardwood forest. *Canadian Journal of Forest Research* 38.1, 82–91. DOI: 10.1139/x07-133.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., and Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11.10, 1065–1071. DOI: 10.1111/j.1461-0248.2008.01219.x.

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M., Wall, D. H., and Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience* 8.10, 776–779. DOI: 10.1038/ngeo2520.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology* 19.4, 988–995. DOI: 10.1111/gcb.12113.

Duiker, S. W., Rhoton, F. E., Torrent, J., Smeck, N. E., and Lal, R. (2003). Iron (Hydr)Oxide Crystallinity Effects on Soil Aggregation. *Soil Science Society of America Journal* 67.2, 606. DOI: 10.2136/sssaj2003.6060.

Dümig, A., Häusler, W., Steffens, M., and Kögel-Knabner, I. (2012). Clay fractions from a soil chronosequence after glacier retreat reveal the initial evolution of organo–mineral associations. *Geochimica et Cosmochimica Acta* 85, 1–18. DOI: 10.1016/j.gca.2012.01.046.

Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10.12, 1135–1142. DOI: 10.1111/j.1461-0248.2007.01113.x.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., Collins, S. L., Davies, K. F., Du, G., Feng, X., Firn, J., Gruner, D. S., Hagenah, N., Hautier, Y., Heckman, R. W., Jin, V. L., Kirkman, K. P., Klein, J., Ladwig, L. M., Li, Q., McCulley, R. L., Melbourne, B. A., Mitchell, C. E., Moore, J. L., Morgan, J. W., Risch, A. C., Schütz, M., Stevens, C. J., Wedin, D. A., and Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants* 1.7, 15080. DOI: 10.1038/nplants.2015.80.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., III, F. S. C., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F., and Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4.6, 471–476. DOI: 10.1038/nclimate2177.

Fitzhugh, R. D., Driscoll, C. T., Groffman, P. M., Tierney, G. L., Fahey, T. J., and Hardy, J. P. (2003). Soil Freezing and the Acid-Base Chemistry of Soil Solutions in a Northern Hardwood Forest. *Soil Science Society of America Journal* 67.6, 1897. DOI: 10.2136/sssaj2003.1897.

García-Palacios, P., Maestre, F. T., Kattge, J., and Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters* 16.8, 1045–1053. DOI: 10.1111/ele.12137.

Groffman, P. M., Hardy, J. P., Driscoll, C. T., and Fahey, T. J. (2006). Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. *Global Change Biology* 12.9, 1748–1760. DOI: 10.1111/j.1365-2486.2006.01194.x.

Groffman, P., Driscoll, C., Fahey, T., Hardy, J., Fitzhugh, R., and Tierney, G. (2001). Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. *Biogeochemistry* 56.2, 191–213. DOI: 10.1023/A:1013024603959.

Grogan, P. and Jonasson, S. (2005). Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Global Change Biology* 11.3, 465–475. DOI: 10.1111/j.1365-2486.2005.00912.x.

Groisman, P. Y. and Gutman, G., eds. (2012). *Regional Environmental Changes in Siberia and Their Global Consequences*. Springer Science + Business Media. DOI: 10.1007/978-94-007-4569-8.

Groisman, P. Y., Blyakharchuk, T. A., Chernokulsky, A. V., Arzhanov, M. M., Marchesini, L. B., Bogdanova, E. G., Borzenkova, I. I., Bulygina, O. N., Karpenko, A. A., Karpenko, L. V., Knight, R. W., Khon, V. C., Korovin, G. N., Meshcherskaya, A. V., Mokhov, I. I., Parfenova, E. I., Razuvaev, V. N., Speranskaya, N. A., Tchebakova, N. M., and Vygodskaya, N. N. (2012). Climate changes in Siberia. In: *Regional Environmental Changes in Siberia and Their Global Consequences*. Chap. 3, 57–109. DOI: 10.1007/978-94-007-4569-8_3.

Güsewell, S. (2004). N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164.2, 243–266. DOI: 10.1111/j.1469-8137.2004.01192.x.

Harmon, M. E., Silver, W. L., Fasth, B., Chen, H., Burke, I. C., Parton, W. J., Hart, S. C., and Currie, W. S. (2009). Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Global Change Biology* 15.5, 1320–1338. DOI: 10.1111/j.1365-2486.2008.01837.x.

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B., and Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters* 14.9, 852–862. DOI: 10.1111/j.1461-0248.2011.01651.x.

Hättenschwiler, S. and Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences* 102.5, 1519–1524. DOI: 10.1073/pnas.0404977102.

Hättenschwiler, S., Tiunov, A. V., and Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 36.1, 191–218. DOI: 10.1146/annurev.ecolsys.36.112904.151932.

Hatton, P.-J., Kleber, M., Zeller, B., Moni, C., Plante, A. F., Townsend, K., Gelhaye, L., Lajtha, K., and Derrien, D. (2012). Transfer of litter-derived N to soil mineral-organic associations: Evidence from decadal 15N tracer experiments. *Organic Geochemistry* 42.12, 1489–1501. DOI: 10.1016/j.orggeochem.2011.05.002.

Hatton, P.-J., Remusat, L., Zeller, B., Brewer, E. A., and Derrien, D. (2015). NanoSIMS investigation of glycine-derived C and N retention with soil organo-mineral associations. *Biogeochemistry* 125.3, 303–313. DOI: 10.1007/s10533-015-0138-8.

Henry, H. A. (2007). Soil freeze–thaw cycle experiments: Trends, methodological weaknesses and suggested improvements. *Soil Biology and Biochemistry* 39.5, 977–986. DOI: 10.1016/j.soilbio.2006.11.017.

IPCC (2013). *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*.

Ed. by T. Stocker, D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. Midgley. Cambridge Books Online. Cambridge University Press. 1535 pp. DOI: 10.1017/CBO9781107415324.

Kampichler, C. and Bruckner, A. (2009). The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews* 84.3, 375–389. DOI: 10.1111/j.1469-185x.2009.00078.x.

Kemmitt, S., Lanyon, C., Waite, I., Wen, Q., Addiscott, T., Bird, N., O'Donnell, A., and Brookes, P. (2008). Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass—a new perspective. *Soil Biology and Biochemistry* 40.1, 61–73. DOI: 10.1016/j.soilbio.2007.06.021.

Kleber, M., Sollins, P., and Sutton, R. (2007). A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. *Biogeochemistry* 85 (1), 9–24. DOI: 10.1007/s10533-007-9103-5.

Kreyling, J., Peršoh, D., Werner, S., Benzenberg, M., and Wöllecke, J. (2012). Short-term impacts of soil freeze-thaw cycles on roots and root-associated fungi of Holcus lanatus and Calluna vulgaris. *Plant and Soil* 353 (1-2), 19–31. DOI: 10.1007/s11104-011-0970-0.

Kuzyakov, Y. and Xu, X. (2013). Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. *New Phytologist* 198.3, 656–669. DOI: 10.1111/nph.12235.

Lavelle, P. and Spain, A. V. (2001). *Soil Ecology*. Springer Netherlands. DOI: 10.1007/978-94-017-5279-4.

Lehmann, J. and Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*. DOI: 10.1038/nature16069.

Lewis, W. M. and Grant, M. C. (1980). Relationships between Snow Cover and Winter Losses of Dissolved Substances from a Mountain Watershed. *Arctic and Alpine Research* 12.1, 11. DOI: 10.2307/1550586.

Lipson, D. A., Schmidt, S. K., and Monson, R. K. (1999). Links between Microbial Population Dynamics and Nitrogen Availability in an Alpine Ecosystem. *Ecology* 80.5, 1623. DOI: 10.2307/176551.

Mambelli, S., Bird, J. A., Gleixner, G., Dawson, T. E., and Torn, M. S. (2011). Relative contribution of foliar and fine root pine litter to the molecular composition of soil organic matter after in situ degradation. *Organic Geochemistry*. DOI: 10.1016/j.orggeochem.2011.06.008.

Mast, M. A., Wickland, K. P., Striegl, R. T., and Clow, D. W. (1998). Winter fluxes of CO_2 and CH4 from subalpine soils in Rocky Mountain National Park, Colorado. *Global Biogeochemical Cycles* 12.4, 607–620. DOI: 10.1029/98gb02313.

McKeague, J. A. and Day, J. H. (1966). Dithionite and oxalate-extractable Fe and Al as aids in differentiating various classes of soils. *Canadian Journal of Soil Science* 46.1, 13–22. DOI: 10.4141/cjss66-003.

Mikutta, R., Schaumann, G. E., Gildemeister, D., Bonneville, S., Kramer, M. G., Chorover, J., Chadwick, O. A., and Guggenberger, G. (2009). Biogeochemistry of mineral–organic associations across a long-term mineralogical soil gradient (0.3–4100kyr), Hawaiian

Islands. *Geochimica et Cosmochimica Acta* 73.7, 2034–2060. DOI: 10.1016/j.gca.2008.12.028.

Mitchell, M. J., Driscoll, C. T., Kahl, J. S., Murdoch, P. S., and Pardo, L. H. (1996). Climatic Control of Nitrate Loss from Forested Watersheds in the Northeast United States. *Environmental Science and Technology* 30.8, 2609–2612. DOI: 10.1021/es9600237.

Monson, R. K., Burns, S. P., Williams, M. W., Delany, A. C., Weintraub, M., and Lipson, D. A. (2006a). The contribution of beneath-snow soil respiration to total ecosystem respiration in a high-elevation, subalpine forest. *Global Biogeochemical Cycles* 20.3. DOI: 10.1029/2005gb002684.

Monson, R. K., Lipson, D. L., Burns, S. P., Turnipseed, A. A., Delany, A. C., Williams, M. W., and Schmidt, S. K. (2006b). Winter forest soil respiration controlled by climate and microbial community composition. *Nature* 439.7077, 711–714. DOI: 10.1038/nature04555.

Muhs, D. (2007). Loess deposits, origins and properties. In: *Encyclopedia of Quaternary Science*, 1405–1418. DOI: 10.1016/b0-44-452747-8/00158-7.

Näsholm, T., Kielland, K., and Ganeteg, U. (2009). Uptake of organic nitrogen by plants. *New Phytologist* 182.1, 31–48. DOI: 10.1111/j.1469-8137.2008.02751.x.

Nielsen, C. B., Groffman, P. M., Hamburg, S. P., Driscoll, C. T., Fahey, T. J., and Hardy, J. P. (2001). Freezing Effects on Carbon and Nitrogen Cycling in Northern Hardwood Forest Soils. *Soil Science Society of America Journal* 65.6, 1723. DOI: 10.2136/sssaj2001.1723.

Orcutt, D. M. and Nilsen, E. T. (2000). *The Physiology of Plants Under Stress: Soil and Biotic Factors*. John Wiley and Sons Inc.

Osler, G. H. R. and Sommerkorn, M. (2007). Toward a complete soil C and N cycle: Incorporating the soil fauna. *Ecology* 88.7, 1611–1621. DOI: 10.1890/06-1357.1.

Pena, R., Tejedor, J., Zeller, B., Dannenmann, M., and Polle, A. (2013). Interspecific temporal and spatial differences in the acquisition of litter-derived nitrogen by ectomycorrhizal fungal assemblages. *New Phytologist* 199.2, 520–528. DOI: 10.1111/nph.12272.

Peters, N. E. and Leavesley, G. H. (1995). Biotic and abiotic processes controlling water chemistry during snowmelt at rabbit ears pass, Rocky Mountains, Colorado, U.S.A. *Water, Air, and Soil Pollution* 79.1-4, 171–190. DOI: 10.1007/bf01100436.

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101.1-3, 133–149. DOI: 10.1007/s10533-010-9439-0.

R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rawlins, A. J., Bull, I. D., Ineson, P., and Evershed, R. P. (2007). Stabilisation of soil organic matter in invertebrate faecal pellets through leaf litter grazing. *Soil Biology and Biochemistry* 39.5, 1202–1205. DOI: 10.1016/j.soilbio.2006.10.010.

Repo, T., Sirkiä, S., Heinonen, J., Lavigné, A., Roitto, M., Koljonen, E., Sutinen, S., and Finér, L. (2014). Effects of frozen soil on growth and longevity of fine roots of Norway spruce. *Forest Ecology and Management* 313, 112–122. DOI: 10.1016/j.foreco.2013.11.002.

Rouifed, S., Handa, I. T., David, J.-F., and Hättenschwiler, S. (2010). The importance of biotic factors in predicting global change effects on decomposition of temperate forest leaf litter. *Oecologia* 163.1, 247–256. DOI: 10.1007/s00442-009-1528-1.

Schimel, J. P. and Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* 85.3, 591–602. DOI: 10.1890/03-8002.

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., and Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature* 478.7367, 49–56. DOI: 10.1038/nature10386.

Sebestyen, S. D., Boyer, E. W., Shanley, J. B., Kendall, C., Doctor, D. H., Aiken, G. R., and Ohte, N. (2008). Sources, transformations, and hydrological processes that control stream nitrate and dissolved organic matter concentrations during snowmelt in an upland forest. *Water Resources Research* 44.12. DOI: 10.1029/2008wr006983.

Sickman, J. O., Leydecker, A., Chang, C. C., Kendall, C., Melack, J. M., Lucero, D. M., and Schimel, J. (2003). Mechanisms underlying export of N from high-elevation catchments during seasonal transitions. *Biogeochemistry* 64.1, 1–24. DOI: 10.1023/a:1024928317057.

St John, T. V. (1980). Influence of litterbags on growth of fungal vegetative structures. *Oecologia* 46.1, 130–132. DOI: 10.1007/bf00346977.

Staaf, H. (1980). Release of plant nutrients from decomposing leaf litter in a South Swedish beech forest. *Ecography* 3.2, 129–136. DOI: 10.1111/j.1600-0587.1980.tb00719.x.

Tierney, G., Fahey, T., Groffman, P., Hardy, J., Fitzhugh, R., and Driscoll, C. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56.2, 175–190. DOI: 10.1023/A:1013072519889.

Tinker, P. B. and Nye, P. H. (2000). *Solute Movement in the Rhizosphere*. Oxford University Press. 370 pp.

Trofymow, J. A., Moore, T. R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M., and Visser, S. (2002). Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Canadian Journal of Forest Research* 32.5, 789–804. DOI: 10.1139/x01-117.

Versini, A., Zeller, B., Derrien, D., Mazoumbou, J.-C., Mareschal, L., Saint-André, L., Ranger, J., and Laclau, J.-P. (2013). The role of harvest residues to sustain tree growth and soil nitrogen stocks in a tropical Eucalyptus plantation. *Plant and Soil* 376.1-2, 245–260. DOI: 10.1007/s11104-013-1963-y.

Virto, I., Barré, P., and Chenu, C. (2008). Microaggregation and organic matter storage at the silt-size scale. *Geoderma* 146.1-2, 326–335. DOI: 10.1016/j.geoderma.2008.05.021.

Vitousek, P. M., Porder, S., Houlton, B. Z., and Chadwick, O. A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications* 20.1, 5–15. DOI: 10.1890/08-0127.1.

von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., and Flessa, H. (2006). Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *European Journal of Soil Science* 57.4, 426–445. DOI: 10.1111/j.1365-2389.2006.00809.x.

Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. E., Dangerfield, J. M., Parton, W. J., Rusek, J., Voigt, W., Wolters, V., Gardel, H. Z., Ayuke, F. O., Bashford, R., Beljakova, O. I., Bohlen, P. J., Brauman, A., Flemming, S., Henschel,

J. R., Johnson, D. L., Jones, T. H., Kovarova, M., Kranabetter, J. M., Kutny, L., Lin, K.-C., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabar, M. G., Salamon, J.-A., Swift, M. J., Varela, A., Vasconcelos, H. L., White, D., and Zou, X. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, 2661–2677. DOI: 10.1111/j.1365-2486.2008.01672.x.

Wallenstein, M. D., McMahon, S. K., and Schimel, J. P. (2009). Seasonal variation in enzyme activities and temperature sensitivities in Arctic tundra soils. *Global Change Biology* 15.7, 1631–1639. DOI: 10.1111/j.1365-2486.2008.01819.x.

Wang, W., Peng, S., Wang, T., and Fang, J. (2010). Winter soil CO_2 efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China. *Soil Biology and Biochemistry* 42.3, 451–458. DOI: 10.1016/j.soilbio.2009.11.028.

Wolters, V. (2000). Invertebrate control of soil organic matter stability. *Biology and Fertility of Soils* 31.1, 1–19. DOI: 10.1007/s003740050618.

Zeller, B., Colin-Belgrand, M., Dambrine, E., and Martin, F. (2001). Fate of nitrogen released from 15N-labeled litter in European beech forests. *Tree Physiology* 21.2-3, 153–162. DOI: 10.1093/treephys/21.2-3.153.

Zeller, B., Colin-Belgrand, M., Dambrine, E., Martin, F., and Bottner, P. (2000). Decomposition of 15N-labelled beech litter and fate of nitrogen derived from litter in a beech forest. *Oecologia* 123.4, 550–559. DOI: 10.1007/pl00008860.

Zeller, B., Colin-Belgrand, M., Dambrine, É., and Martin, F. (1998). 15N partitioning and production of 15N-labelled litter in beech trees following [15N]urea spray. *Annals of Forest Science* 55.3, 375–383. DOI: 10.1051/forest:19980308.

Zeller, B. and Dambrine, E. (2011). Coarse particulate organic matter is the primary source of mineral N in the topsoil of three beech forests. *Soil Biology and Biochemistry* 43.3, 542–550. DOI: 10.1016/j.soilbio.2010.11.019.

Zhang, D., Hui, D., Luo, Y., and Zhou, G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology* 1.2, 85–93. DOI: 10.1093/jpe/rtn002.

Zhang, T. (2005). Influence of the seasonal snow cover on the ground thermal regime: An overview. *Reviews of Geophysics* 43.4. DOI: 10.1029/2004rg000157.

Chapter 8

Discussion

This study provided insights on the biogeochemical cycling and the plant-availability of water and nutrients, and their relation to climate and soil properties, in contrasting SW Siberian ecosystems. SW Siberia historically concentrated agriculture and populations. In the context of global change, the fate of human activities in the region will depend notably on the evolution of the conditions necessary for plant growth. Thus, understanding the drivers of vegetation growth and their relation to changing environmental conditions is of primary importance.

We considered the issue of the impacts of global change on primary production in SW Siberia with a multidisciplinary approach. Our intention was to provide parts of the answer for several broad questions. We also identified some ecological processes that need further investigations.

8.1 Responses to the questions addressed

8.1.1 How does climate regulate tree growth in contrasting pedoclimatic conditions in SW Siberia? In particular, has snow a noticeable influence on tree growth? Has average tree growth changed in the recent decades?

Our dendroclimatic analysis revealed that aspen stem radial growth responded to different climate variables depending on the pedoclimatic context. Overall, it was possible to distinguish two groups of sites according to the climate–growth relationships: the sites located in steppe/southern forest-steppe, typically the south of SW Siberia, and the sites located in northern forest-steppe/sub-taiga, typically the north of SW Siberia.

In steppe/southern forest-steppe, which experience drier climatic conditions, aspen stem radial growth was mostly sensitive to the soil water budget in summer: growth was enhanced by high precipitations, and reduced by high air and soil temperatures, and by water deficits. Water budget had persistent effects over time, impacting growth at least in the following year. Early and late growing season high

temperatures tended to enhance tree growth, suggesting the length of the growing season also matters at these sites.

In the north of forest-steppe/sub-taiga, aspen stem radial growth was essentially stimulated by high summer air and soil temperatures, possibly because they enhance water and nutrient absorption (enhancement of mineralization, mass flow and diffusion). However, high early spring air and soil temperatures negatively impacted tree growth. A possible explanation is a de-synchronization between the moment of high nutrient availability (spring-flush hypothesis) and the period of plant uptake.

At almost all sites, tree growth responded positively to snow height of the winter preceding the previous growing season. Such a response may reflect the importance of the water budget of the preceding year, but it is surprising that the effect of snow was not observed also for the immediately following growing season. Also, our northern sites did not exhibit any response to water budget. To date, we did not find any convincing hypothesis that could explain such a phenomenon. However, the negative impacts of snow cover at the beginning and the end of the snow season—yet not clearly observed at all sites—suggest that early and late snowfalls are associated with shorter growing season.

In addition to the questions we addressed, we found that the average stem radial growth levels at a given age tend to be higher in the forest-steppe zone, typically the south of SW Siberia, than in the sub-taiga zone, typically the northern part. This suggests a higher fertility of the sites located in forest-steppe, possibly due to climatic conditions (higher temperature, longer vegetation season) and/or soil properties. However, this information needs to be verified with a thorough sampling design and the checking of additional indicators. For instance, a relatively simple indicator of site fertility is the mean tree height of dominant and co-dominant trees at a given age and for a given period, it is often referred as "site index" (Chen et al. 1998, 2002; Leonelli et al. 2008; Skovsgaard and Vanclay 2008). Our data set was not sufficiently robust to rely on the site indexes computed. Ideally, it is necessary to have a balanced design (i.e. even-aged stands for a given date at all study sites) and to measure much more trees.

Finally, all our study sites presented a trend of increasing stem radial growth in the recent decades. Again, this information requires to be confirmed with a more robust sampling design. Also, a major uncertainty remains, the evolution of the social status of the sampled trees along their life, but it will be impossible to check this without long-term monitoring sites. Despite these limitations, our results suggest that recent global change rather had the tendency to alleviate growth limitation(s) than to exacerbate them. Possible explanations include: warmer temperatures, longer vegetation season, rising atmospheric CO_2 levels, enhanced nutrient availability through atmospheric deposition (nitrogen) or stimulation of decomposition processes.

8.1.2 What are the current soil temperature and moisture regimes in forest-steppe and sub-taiga? How are climate variations, and in particular snow depth, susceptible to influence these regimes in contrasting pedoclimatic situations?

We monitored the soil temperature and moisture regimes under ambient and experimentally increased snow height at Barnaul and Tomsk, two sites of SW Siberia presenting different climate and soil conditions. Modelling permitted to reconstruct the soil water budget from the last 46 years and to simulate its possible evolution under different scenarii. Contrasting soil temperature and moisture regimes were characterized between these two sites.

On the two sites, the soil temperature dynamics are tightly coupled with air temperature while the soil is not covered by snow. Usually, at Tomsk (in the north of SW Siberia, sub-taiga), the snow-cover is higher and the soil does not freeze in winter. At Barnaul (south of SW Siberia, forest-steppe) the snow cover is lower and the soil freezes. In summer, soil temperature is generally higher in the south. If snow height increases with climate change, soil freezing may be attenuated in the south of SW Siberia. However, this could be modulated by later apparition of the seasonally permanent snow-pack. In fact, the overall winter soil thermal status greatly depends on the thermal status at the setting of the snow-cover. Concretely, when the snow-pack appears late, soil is likely to be already frozen due to the low air temperature of late-autumn in Siberia. Also, if the soil moisture content decreases, soil is more prone to freeze.

The time course of the water budget through seasons is similar between our sites. However, processes differ essentially in intensity, modulated by the joined effects of climate, soil properties and vegetation. In both sites, the soil moisture content is depleted in summer. This depletion is much stronger in the south, frequently leading to water deficits. In the north, autumn precipitation often permit a complete recharge of the soil water reserve while, in the south, the snow-melt is important to re-fill it. In the north, since the soil is quickly saturated at snow-melt, and since there is more snow, our simulations indicate a greater drainage than in the south. However, in water-saturated situations, surface runoff may also occur and the partitioning between drainage and runoff is of major importance for biogeochemical cycling. Drainage was not measured in our sites and remains a major uncertainty.

Our simulations suggest an increase of water limitations in both forest-steppe and sub-taiga with climate change. This phenomenon would be driven by warmer temperatures and earlier vegetation seasons and be modulated by the amounts of winter precipitation, i.e. snow. In the south, long and intense water shortages are likely to become the usual situation. In the north, they may appear and occur at

higher frequency but, even under the current southern climatic conditions, water stress might be modulated by soil properties. In both cases, an earlier vegetation season would increase the water depletion of the soil profile, and induce earlier apparition, longer duration, and higher intensity of water-stress.

Variations in snow cover may impact different components of the soil water budget, and in different ways, between forest-steppe and sub-taiga. The soil water content over the year would be dependent on the amount of snow in forest-steppe while it would not be impacted in sub-taiga. In both sites, the drainage is likely to substantially decrease if the snow levels are decreasing or maintained while only a gentle increase is expected with a sharp increase of snow levels (current winter precipitation ×1.5). In any case, almost all the yearly drainage will occur at snow-melt.

The question of drainage requires further investigations in SW Siberia. Measurements of drainage amounts below the soil profile explored by fine roots would help understanding the fate of melt-water. The measurement of nutrient concentrations in drained water would inform on the possible losses induced by snow processes.

8.1.3 Do contrasting climate and soil conditions lead to diverging fine root distributions in SW Siberia?

Measurements of the distribution of fine root length and mass throughout the soil profile revealed that, in general, fine root exploration was deeper and total length and mass were higher in forest-steppe than in sub-taiga. Since these patterns were consistent between contrasting vegetation covers, namely aspen forest and grassland, they can be related to pedoclimatic conditions. Two types of factors could explain these broad patterns: resources foraging and physical constraints of the environment.

The role of nutrient availability is discussed below. In steppe/forest-steppe, deeper fine root systems may reflect a strategy for water acquisition because soil dessication is usually important in summer. On the contrary, in sub-taiga, regular water saturation of the soil profile, persistent over long periods in the subsurface soil, may constitute a physical constraint to fine root development deep in the soil profile. Other environmental constraints were detected on the local scale, such as a shallow bedrock, however they are neither variables of global change, nor limiting factors of primary production in our study sites. Also, we proposed that soil freezing in steppe/forest-steppe, in relation to shallow snow cover, could also promote deeper development of fine roots because of increased mortality in surface. As far as we know, such effect on fine root profile has never been reported and need further testing. Perhaps, freezing is more likely to enhance the turnover of fine roots.

We also observed patterns attributed to the vegetation types. Fine root exploration

tended to be deeper in forest than in grassland, and for trees than for understorey vegetation within forest stands. Additionally, species and communities have different traits, among which differing root quality and decomposability, that impact plant–soil interactions and biogeochemical cycles (Bardgett et al. 2014; Freschet et al. 2012; Guo et al. 2008; Kong et al. 2014; Prieto et al. 2016; Roumet et al. 2016, 2006; Smith et al. 2014). For example, it was suggested that land conversion from forest to agriculture leads to changes in root functional traits that enhance root decomposition rates and could induce soil carbon losses (Prieto et al. 2016). Further investigations on plant root traits would thus provide insights on the ecological consequences of land cover changes in SW Siberia.

Besides the distribution of fine roots within the soil profile, their dynamics is a key component in the biogeochemical cycling of carbon and nutrients (Clemmensen et al. 2013; Ruess et al. 2003; Yuan and Chen 2010; Yuan et al. 2011). The investigation of fine root production and turnover would thus be of major interest in SW Siberia since they are greatly controlled by factors varying along with global change (Brunner and Godbold 2007; Finér et al. 2011; Gill and Jackson 2000; McCormack et al. 2013; McCormack and Guo 2014).

Finally, roots are not active the same way throughout the profile, depending on water and nutrient availability and interactions among the plant communities. It would be interesting to know the depth of active uptake across the seasons, and if different species have different strategies for water acquisition in SW Siberia. Water isotopy analyses (seasonal samplings of soil and below- and above-ground vegetation parts) are ongoing in our study sites.

8.1.4 What is the phosphorus status of SW Siberian soils? Which amount of phosphorus is available for plants?

The concentrations, the stocks, and the distribution of the different phosphorus (P) pools we measured over the soil profile were relatively homogeneous on the scale of SW Siberia.

The early stage of soil formation, coupled with slow kinetics of pedogenesis, have probably not yet conducted to a sufficiently wide range of soil physico-chemical conditions to observe more diverging P status (for example, a gradient of P status along with the gradient of climate, fine root exploration, and soil-forming processes that exists in SW Siberia). However, some of the variations in P pools at given depths can be explained by soil properties (e.g. accumulation of clays, oxides and/or carbonates) that result from soil-forming processes. This suggests that the diverging soil-forming processes may induce differences in soil P status in the long term.

The comparison of these SW Siberian P levels to similar vegetation contexts on the global scale revealed high to very high levels of total, organic and inorganic P in

topsoils. These results seem to be generalizable to Northern Eurasia but additional measurements are required to verify this statement. The amount of plant-available P in topsoils, evaluated as isotopically exchangeable phosphate ions, was intermediate on the global scale. However, large stocks of isotopically exchangeable phosphate ions are stored in the subsurface layers where fine root exploration is currently low. These results suggest that the P resource is unlikely to constrain vegetation growth and agricultural development in the present and near future conditions.

Finally, the relative contribution of mineral weathering and organic matter decomposition in providing exchangeable phosphate ions in the soils of SW Siberia remains an open question.

8.1.5 Is the liberation of nitrogen from the leaf-litter driven by climatic conditions? Is the fate of N in the soil controlled by climate?

Our monitoring of the fate of ^{15}N derived from leaf-litter decomposition within different ecosystem compartments revealed contrasting patterns both between and within sites. Between sites, the different patterns can be related to climate and soil conditions, they are consistent for both aspen forest and grassland. We identified two groups of sites closely related to the bioclimatic zones studied (forest-steppe and sub-taiga). Within sites, we observed differing N dynamics between forest and grassland, they can be related to differing chemical composition of initial litter and plant–soil interactions.

On the time scale of our study (three years), we observed, along with faster decay rates, faster releases of leaf litter-N in sub-taiga than in forest-steppe. As such, higher quantities of N were retrieved in the soil and the penetration was deeper in sub-taiga. Deeper penetration may be related to water dynamics. Notably, the drainage is more intense in sub-taiga because of higher snow levels. Interestingly, these higher drainage seem to not induce a too large loss of N from the system. As an explanation, we propose that the soils from sub-taiga are efficient in retaining N. Such retention could result from soil physico-chemical properties (higher fine silt and oxides contents) enhancing soil organic matter stabilization, and/or by the immobilization of N in microbial metabolites. This hypothesis requires further investigations. In particular, it would be interesting to know in which form(s) N is released and retained in the soil (Hatton et al. 2012, 2015; Zeller and Dambrine 2011). For example, we expect ammonium and microbial products to be more associated with clay mineral surfaces than plant N.

In a general manner, N was retained in the first centimetres of the mineral soil in grassland while it was penetrating deeper in forest. Such a phenomenon has certainly to be related to different plant–soil interactions and vegetation cover phenology. As

fine root exploration is denser in grassland topsoil than in forest topsoil, we suppose that an efficient uptake of N by grasses in the first soil layers limits N migration down the profile. It is also possible that grasses are active earlier in the season than trees and understorey species, when there is a stronger potential of drainage because snow-melt saturated the soil.

8.2 Integrated biogeochemical functioning of SW Siberian ecosystems and climate change prospectives

Altogether, our investigations revealed contrasting biogeochemical processes in the forest-steppe and the sub-taiga bioclimatic zones of SW Siberia. In forest-steppe, winter is cold and soil freezes because of shallow snow cover. Snow melt-water constitutes the major input of water into the soil. Summer is warm and dry, frequently leading to soil water deficits. Aspen stem radial growth is sensitive to this soil water budget, and fine root distribution occurs deeper in the soil profile to mine water. The release of organic N, and likely organic P, depend on litter and soil organic matter decomposition. The latter are slowed down by harsh winter and summer conditions that do not favour decomposer activities.

In the sub-taiga, thick snow-pack prevents soil from freezing. Snow melt-water generally induces drainage because soil water reserves are almost filled by autumn precipitation. There is no drought in summer impacting aspen stem radial growth. Thus, it is mainly limited by the length of the vegetation season and summer temperature. As water remains available in topsoil over summer, and is in excess in deep layers, fine roots concentrate in the top layers. The pedoclimatic conditions allow fast above-ground litter degradation and fast incorporation of litter residues into the top mineral soil layers. Snow-melt drainage may export nutrients in soluble forms. However soil properties and the persistence of a basal microbial activity over winter may efficiently immobilize litter-derived N in top horizons.

Climate observations and projections indicate a warming of air temperature and variations in the seasonality of precipitation. While summer precipitation remains stable but occurs less regularly, winter precipitation is increasing, leading to a higher snow-pack.

In forest-steppe, water shortages in soil will become more frequent, more intense, and longer. This will probably induce a deepening of fine root distribution. Winter precipitation will be of crucial importance for the soil water budget. These altered soil temperature and moisture regimes are likely to slow down the turnover of organic matter and the subsequent release of nutrients. A major uncertainty concerns soil freezing in winter. Only a thicker snow-pack appearing early in the

winter, on an unfrozen soil, could be favourable to microbial activity and organic nutrient availability. The overall impact of climate change on vegetation growth and productivity is difficult to assess because of contradictory effects on biogeochemical processes.

In sub-taiga, water shortage may appear from time to time in summer. The increase in winter precipitation may increase drainage unless the soil water reserve was depleted in the previous vegetation season. In this case, snow melt-water will recharge the depleted horizons. Possibly, fine roots will develop deeper to get water. It is likely that soil temperature rise and sufficient water availability will stimulate microbial activity and fasten the turnover of organic matter and the release of its nutrients. These combined effects will likely induce higher vegetation productivity.

References

Bardgett, R. D., Mommer, L., and Vries, F. T. D. (2014). Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology and Evolution* 29.12, 692–699. DOI: 10.1016/j.tree.2014.10.006.

Brunner, I. and Godbold, D. L. (2007). Tree roots in a changing world. *Journal of Forest Research* 12 (2), 78–82. DOI: 10.1007/s10310-006-0261-4.

Chen, H. Y., Klinka, K., and Kabzems, R. D. (1998). Site index, site quality, and foliar nutrients of trembling aspen: relationships and predictions. *Canadian Journal of Forest Research* 28.12, 1743–1755. DOI: 10.1139/x98-154.

Chen, H. Y., Krestov, P. V., and Klinka, K. (2002). Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. *Canadian Journal of Forest Research* 32.1, 112–119. DOI: 10.1139/x01-179.

Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A., and Lindahl, B. D. (2013). Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. *Science* 339.6127, 1615–1618. DOI: 10.1126/science.1231923.

Finér, L., Ohashi, M., Noguchi, K., and Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* 262.11, 2008–2023. DOI: 10.1016/j.foreco.2011.08.042.

Freschet, G. T., Aerts, R., and Cornelissen, J. H. C. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology* 26.1, 56–65. DOI: 10.1111/j.1365-2435.2011.01913.x.

Gill, R. A. and Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147.1, 13–31. DOI: 10.1046/j.1469-8137.2000.00681.x.

Guo, D., Li, H., Mitchell, R. J., Han, W., Hendricks, J. J., Fahey, T. J., and Hendrick, R. L. (2008). Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* 177.2, 443–456. DOI: 10.1111/j.1469-8137.2007.02242.x.

Hatton, P.-J., Kleber, M., Zeller, B., Moni, C., Plante, A. F., Townsend, K., Gelhaye, L., Lajtha, K., and Derrien, D. (2012). Transfer of litter-derived N to soil mineral-organic associations: Evidence from decadal 15N tracer experiments. *Organic Geochemistry* 42.12, 1489–1501. DOI: 10.1016/j.orggeochem.2011.05.002.

Hatton, P.-J., Remusat, L., Zeller, B., Brewer, E. A., and Derrien, D. (2015). NanoSIMS investigation of glycine-derived C and N retention with soil organo-mineral associations. *Biogeochemistry* 125.3, 303–313. DOI: 10.1007/s10533-015-0138-8.

Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H., and Guo, D. (2014). Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* 203.3, 863–872. DOI: 10.1111/nph.12842.

Leonelli, G., Denneler, B., and Bergeron, Y. (2008). Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Canadian Journal of Forest Research* 38.5, 1211–1222. DOI: 10.1139/x07-227.

McCormack, M. L., Eissenstat, D. M., Prasad, A. M., and Smithwick, E. A. H. (2013). Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biology* 19.6, 1697–1708. DOI: 10.1111/gcb.12163.

McCormack, M. L. and Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science* 5. DOI: 10.3389/fpls.2014.00205.

Prieto, I., Stokes, A., and Roumet, C. (2016). Root functional parameters predict fine root decomposability at the community level. *Journal of Ecology*. DOI: 10.1111/1365-2745.12537.

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K.-f., and Stokes, A. (2016). Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist*. DOI: 10.1111/nph.13828.

Roumet, C., Urcelay, C., and Diaz, S. (2006). Suites of root traits differ between annual and perennial species growing in the field. *New Phytologist* 170.2, 357–368. DOI: 10.1111/j.1469-8137.2006.01667.x.

Ruess, R. W., Hendrick, R. L., Burton, A. J., Pregitzer, K. S., Sveinbjornssön, B., Allen, M. F., and Maurer, G. E. (2003). Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs* 73.4, 643–662. DOI: 10.1890/02-4032.

Skovsgaard, J. P. and Vanclay, J. K. (2008). Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. *Forestry* 81.1, 13–31. DOI: 10.1093/forestry/cpm041.

Smith, S. W., Woodin, S. J., Pakeman, R. J., Johnson, D., and Wal, R. van der (2014). Root traits predict decomposition across a landscape-scale grazing experiment. *New Phytologist* 203.3, 851–862. DOI: 10.1111/nph.12845.

Yuan, Z. Y. and Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. *Critical Reviews in Plant Sciences* 29.4, 204–221. DOI: 10.1080/07352689.2010.483579.

Yuan, Z., Chen, H. Y., and Reich, P. B. (2011). Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. *Nature Communications* 2, 344. DOI: 10.1038/ncomms1346.

Zeller, B. and Dambrine, E. (2011). Coarse particulate organic matter is the primary source of mineral N in the topsoil of three beech forests. *Soil Biology and Biochemistry* 43.3, 542–550. DOI: 10.1016/j.soilbio.2010.11.019.

Appendix A

A latitudinal response of aspen growth to climate along a pedoclimatic gradient in south-western Siberia

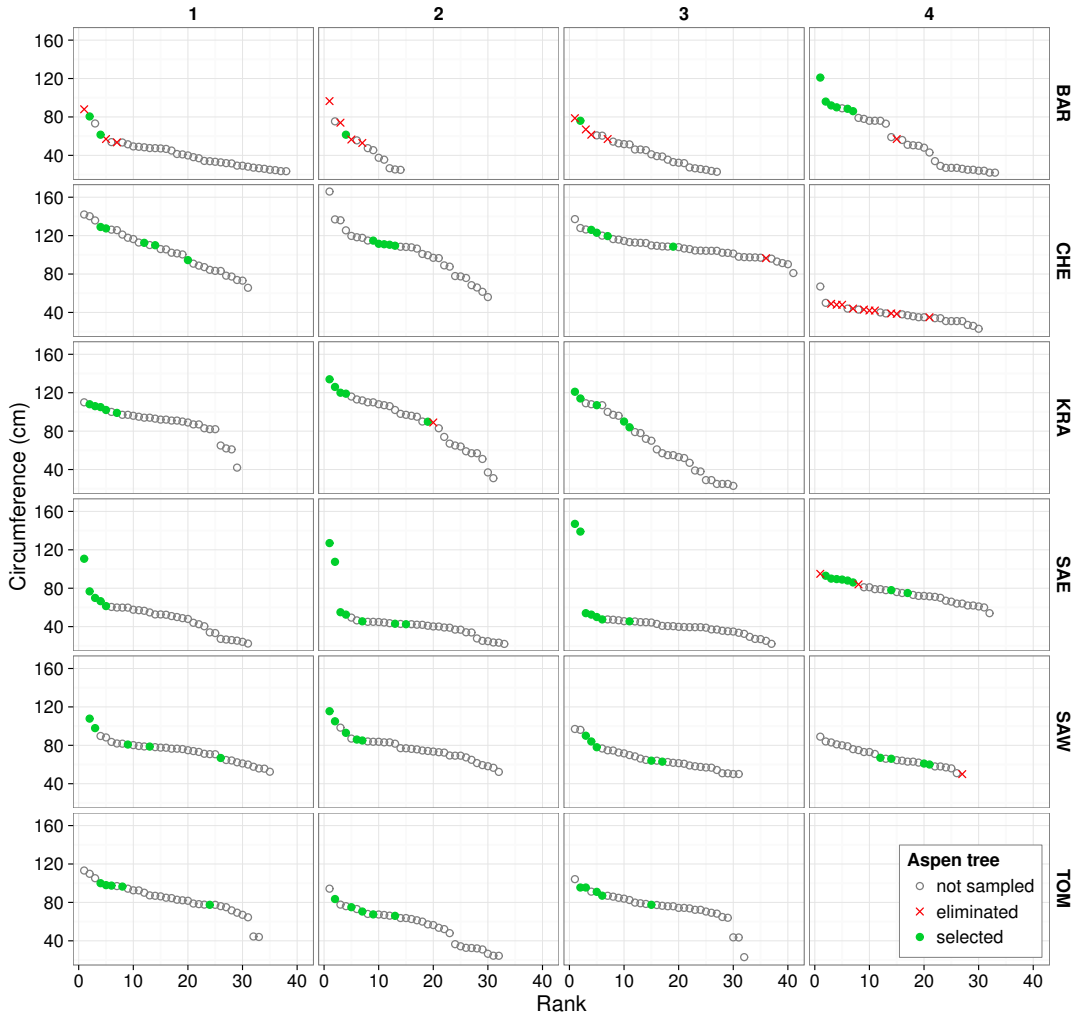


Figure A.1: Circumference and rank of all the aspen trees present on the study stands. About 5 trees were sampled in each study stand (1–4), most of them were used for the analysis between radial-growth and climate (green dots) but some were discarded at the crossdating stage (red crosses).

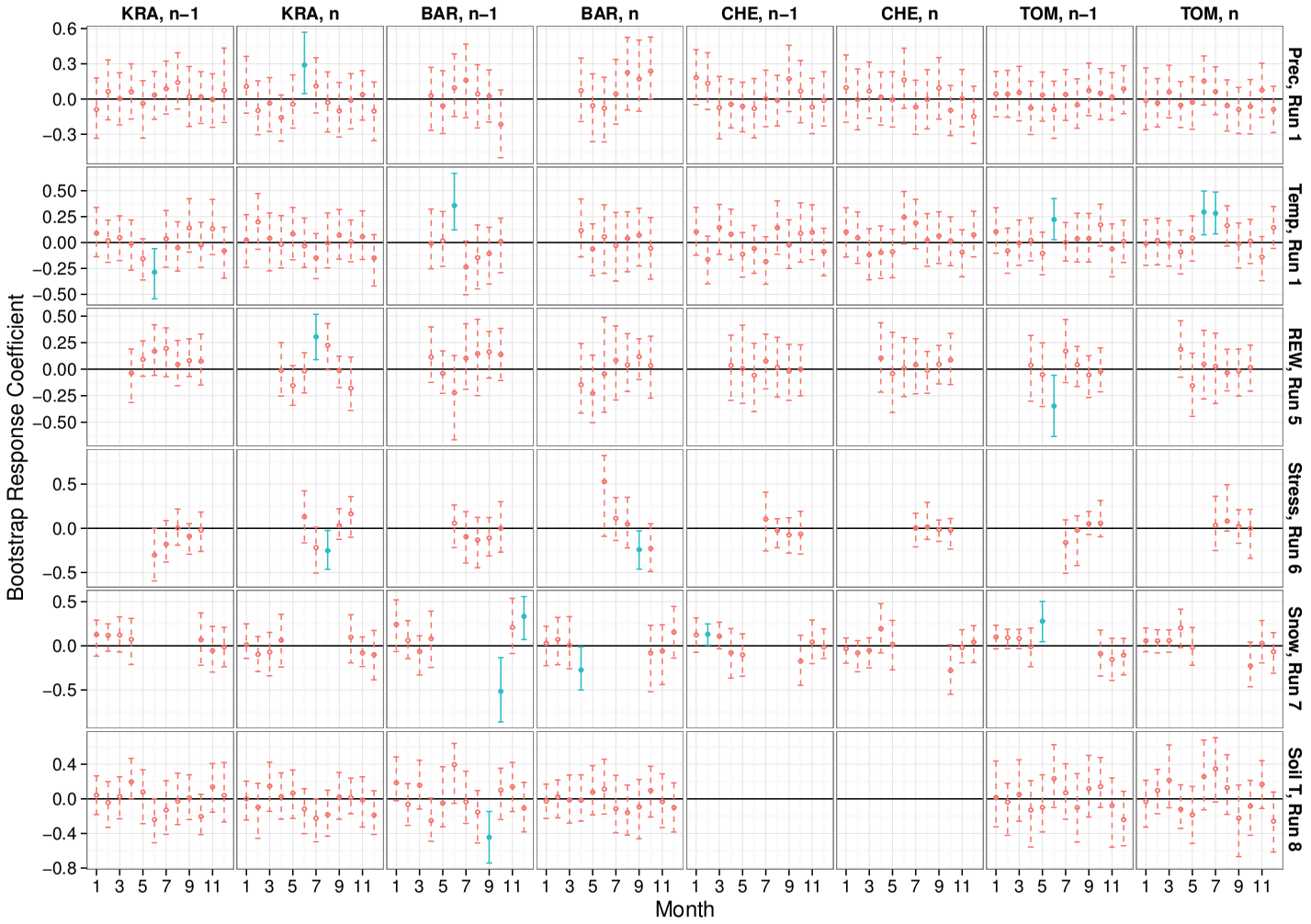


Figure A.2: Plot of the bootstrapped response function analysis relating tree-ring growth to climate-related variables of the current (n) and the previous (n-1) year in four sites of SW Siberia. Significant coefficients, as judged by the bootstrapping procedure, are displayed in blue while non-significant coefficients are in red. The runs are described in Table 3.4.

Table A.1: Composition of the understorey vegetation in forest (herbaceous, shrub and tree species with a height < 1.3 m and a diameter < 1 cm). Range of the number of species over 3 forest stands and dominant species.

Site	Nb of species	Dominant species[a]
BAR	14–18	*Populus tremula* L., *Heracleum sibiricum* L.
CHE	21–27	*Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth
SAE	20–44	*Populus tremula* L., *Carex pallescens* L., *Phlomis tuberosa* L.
SAW	11–17	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth, *Urtica dioica* L.
TOM	16–29	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth

[a]we retained species occurring in at least 2 of the 3 site replicates and with a mean score on the Braun-Blanquet scale > 1

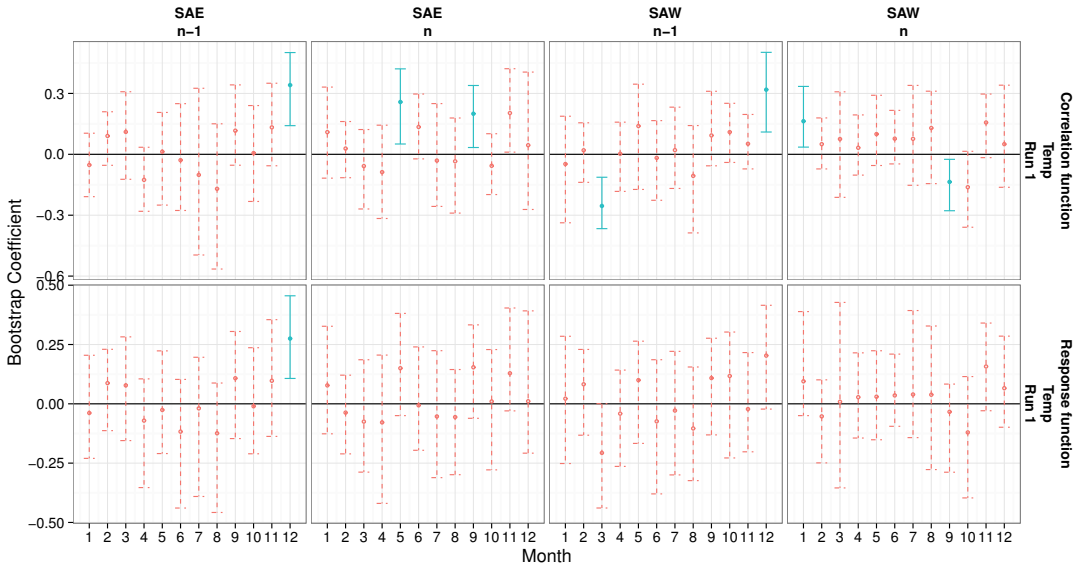


Figure A.3: Plot of the bootstrapped correlation/response function analysis relating tree-ring growth to climate-related variables of the current (n) and the previous (n-1) year for the sites SAE and SAW. Significant coefficients, as judged by the bootstrapping procedure, are displayed in blue while non-significant coefficients are in red. The runs are described in Table 3.4.

Table A.2: Input parameters to the water budget model BILJOU.

Site	Input parameters							
Vegetation parameters								
	Budburst	Fall	LAI_{max}					
BAR	122	288	4.94					
CHE	140	284	3.77					
KRA	115	295	3.84					
TOM	157	280	3.9					
Soil parameters								
	Depth	Roots	W_{fc}	W_{wp}	AD	RD	ah	bh
BAR	23	39	41.68	0.16	1.13	2.4	0	1.65
	49	28	44.77	0.15	1.21	2.4	0	1.65
	85	21	53.05	0.15	1.28	2.5	0	1.70
	120	12	41.70	0.13	1.44	2.5	0	1.70
CHE	26	63	54.03	0.15	0.95	2.4	0	1.48
	42	17	30.10	0.12	1.22	2.4	0	1.58
	83	16	41.55	0.16	1.45	2.5	0	1.63
	120	4	38.96	0.14	1.47	2.5	0	1.63
KRA	18	47	32.81	0.21	0.85	2.4	0	1.48
	41	30	38.77	0.15	1.18	2.4	0	1.58
	67	14	31.67	0.14	1.41	2.5	0	1.63
	120	9	59.89	0.10	1.59	2.5	0	1.63
TOM	20	65	39.44	0.16	1.02	2.4	0	1.30
	49	22	56.17	0.12	1.23	2.4	0	1.50
	74	12	28.10	0.15	1.47	2.5	0	1.55
	120	1	28.38	0.19	1.45	2.5	0	1.55

Budburst: day of leaf apparition (julian day)
Fall: day of leaf abscission (julian day)
LAI_{max}: maximum leaf area index
Depth: depth of the bottom of the soil layer (cm)
Roots: fine root proportion (%)
W_{fc}: water content at the field capacity (mm)
W_{wp}: water content at the wilting point (mm)
AD: apparent density; RD: real density
ah bh: micro- and macro-porosity (the latter controls preferential flow)

Table A.3: Pointer years: years with at least 70 % of the series presenting an absolute relative radial growth variation higher than 10 % relatively to the previous year (Becker et al. 1994). Only years with at least 5 trees available are shown.

Year	BAR	CHE	KRA	SAE	SAW	TOM	Year	BAR	CHE	KRA	SAE	SAW	TOM
1942						+	1978		.	.	.	.	.
1943						.	1979		.	+	.	−	+
1944						.	1980		−	.	.	+	.
1945						.	1981		−	.	−	−	−
1946						.	1982		.	.	.	.	+
1947						−	1983		.	−	.	.	.
1948						.	1984	.	.	+	.	−	.
1949						.	1985	+	.	.	.	.	.
1950						+	1986	.	.	.	.	.	−
1951						.	1987	.	.	−	.	.	.
1952		+				.	1988	.	.	.	.	.	−
1953		+				.	1989	.	.	.	.	.	.
1954		.				−	1990	.	.	.	.	.	.
1955		.				.	1991	.	.	.	.	.	.
1956		+				.	1992	.	.	.	.	.	+
1957		.				−	1993	.	.	.	.	.	.
1958		.				.	1994	.	.	−	.	.	.
1959		.				.	1995	.	−	.	.	.	.
1960		.				.	1996	−	.	.	.	−	−
1961		.				−	1997	+	−	.	.	−	.
1962		+		.		+	1998	.	+	−	.	+	+
1963		−		−		−	1999	.	.	.	.	.	.
1964		+		+		.	2000	.	−	.	.	+	−
1965		−	.	.		.	2001	.	+	+	+	.	+
1966		.	.	.		+	2002	.	+	.	.	.	.
1967		.	.	.	.	.	2003	.	.	−	−	−	−
1968		−	.	.	.	−	2004	.	−	.	.	.	.
1969		.	.	.	.	.	2005	.	.	.	.	+	+
1970		.	+	.	+	−	2006	.	.	.	.	.	.
1971		.	.	.	−	.	2007	−	.	.	.	.	.
1972		+	.	.	.	+	2008	−	.	.	.	.	.
1973		.	.	.	.	+	2009	+	−	.	.	−	−
1974		.	−	.	.	.	2010	−	+	.	.	.	.
1975		.	+	.	−	−	2011	+	.	.	.	.	+
1976		.	.	+	+	+	2012	.	.	.	.	.	+
1977		.	−	.	.	−							

"+" positive pointer year; "−" negative pointer year;
"." not a pointer year; " " data not available

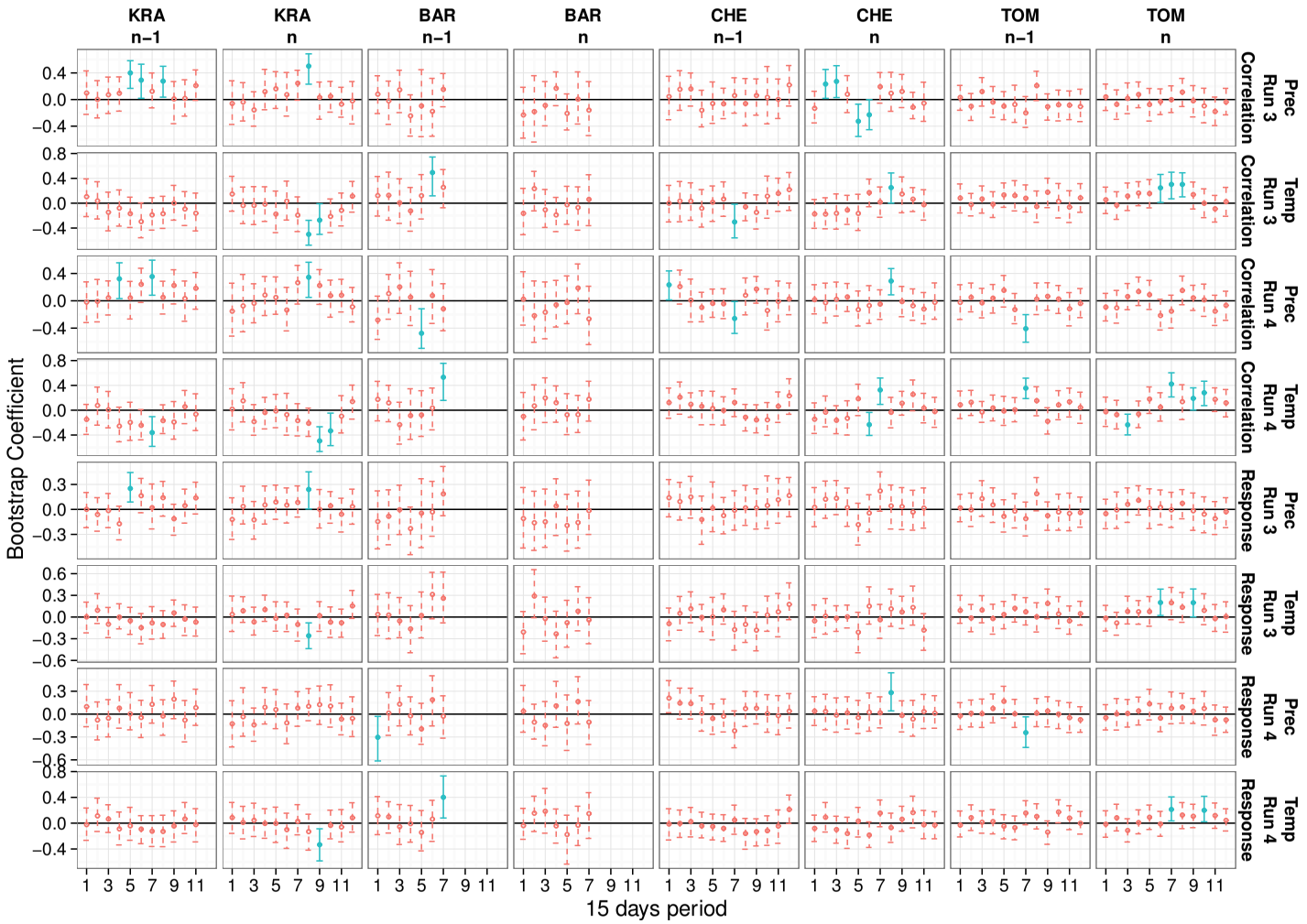


Figure A.4: Plot of the bootstrapped correlation/response function analysis relating tree-ring growth to climate-related variables of the current (n) and the previous (n-1) year on a 15 days time step. In the Run 3, the 15 days time steps start at the snow-melt while, in the Run 4, they start in March. Significant coefficients, as judged by the bootstrapping procedure, are displayed in blue while non-significant coefficients are in red. The runs are described in Table 3.4.

Appendix B

Is snow a hot variable? The control of soil temperature and moisture dynamics in south-western Siberia – Snow manipulation experiment and simulations of soil water budget

B.1 Calibration of the soil moisture sensors

The EC-5 Soil Moisture Sensor (Decagon, USA) determines volumetric water content (VWC) by measuring the dielectric constant of the media using capacitance/frequency domain technology. Its measurement volume is approximately 0.2 L. To improve the accuracy of field VWC measurements, we calibrated the EC-5 sensor with our study soils. At each site, for each vegetation cover and for each depth, we collected vertically a soil cylinder (7 cm diameter, 10 cm height). The cylinders were saturated with water and equipped each with an EC-5 sensor. The sensor signal was recorded every 30 min and we weighed the system (cylinder, soil and equipments) twice a day until reaching a constant weight. At the end of this evaporation phase, the soil was removed from the cylinder and oven-dried at 110 °C to constant weight. To obtain calibration equations, we fitted polynomial and linear equations between the VWC measured by mass difference between wet and dry soil and the VWC reported by the sensor during the evaporation experiment. For the 8 soil layers studied, the best fit was obtained with a polynomial equation (Fig. B.1).

The field VWC raw measurements were corrected using the polynomial equation unless they were out of the domain of calibration (in our case, above the VWC at saturation experimentally determined). In the latter case, raw VWC was corrected using the linear equation in order to minimize the potential error (see the deviation on Fig. B.1). Departures from the domain of calibration could be explained by the spatial variability of soil properties. We also note that they generally occur at the period of snow-melt, when important quantities of water are delivered into the soil.

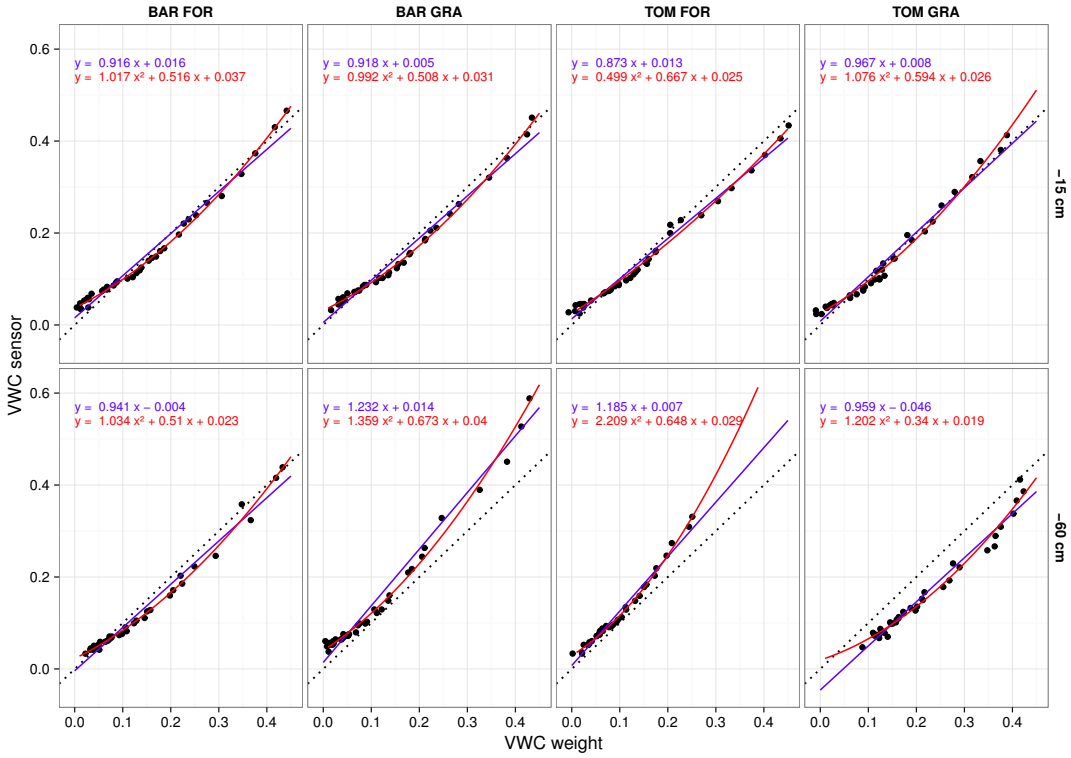


Figure B.1: Calibration of the Decagon EC-5 Soil Moisture Sensor with the soil layers studied at BAR and TOM aspen forest (FOR) and grassland (GRA). Soil volumetric water content (VWC) reported by the sensor is plotted against soil VWC measured weighing the mass of water in the sample. We fitted linear (blue) and polynomial (red) equations.

B.2 Additional information on the constitution of climate data sets

Wind speed The wind speed at 2 m above the soil surface (W_{2m}) was computed from the wind speed measured at 10 m (W_{10m}) as following:

$$W_{2m} = W_{10m} \times \frac{4.87}{\ln(67.8 \times 10 - 5.42)} \tag{B.1}$$

Vapour pressure deficit The vapour pressure deficit (VPD) was computed as following:

$$VPD = \left(1 - \frac{H}{100}\right) \times 5.999 \times \exp[7.062 \times \log(1 + 0.01063 \times T_{mean})] \tag{B.2}$$

where H is the relative air humidity (in %) and T_{mean} is the daily mean temperature (in °C).

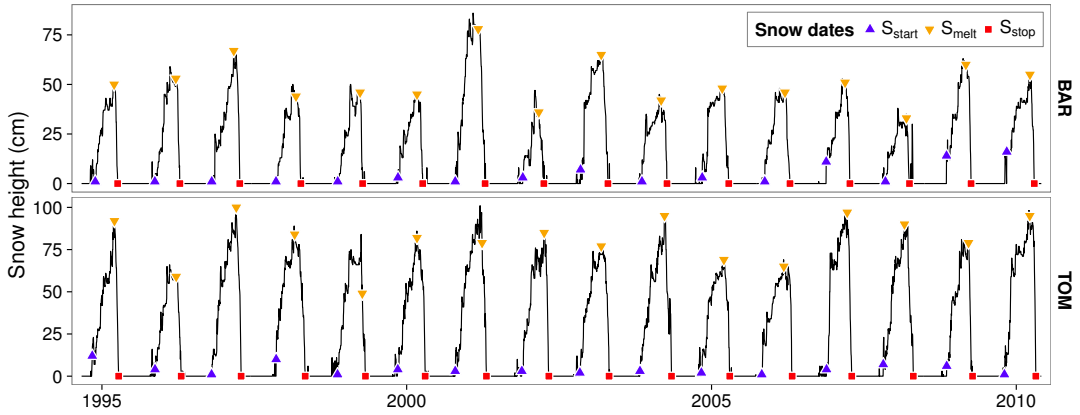


Figure B.2: Determination of the key dates of the snow-pack: date of the apparition of the continuous and seasonally permanent snow pack (S_{start}), date where the snow pack starts to melt until its disappearance (S_{melt}), and date of the disappearance of the continuous and seasonally permanent snow pack (S_{stop}). The figure shows the fit of the empirically determined dates for the period 1995–2010 at BAR and TOM. The quality of the fit for the other years of the period 1966–2015 was similar.

Global radiation The data set of global radiation for Omsk contains several gaps of short duration (days). We filled those gaps with the average value for the same day of the year. Global radiation were not available for the entire years 2014 and 2015 at the date of the analysis, we used the values of the year 2013.

Winter precipitations To take into account the year to year variability, we empirically defined, for each winter, three characteristic dates of the snow pack on the base of snow height measurements provided by RIHMI-WDC. The date of the apparition of a continuous and seasonally permanent snow pack (S_{start}) was defined as the earliest day of the winter from which the snow height does not go back to 0 cm by the end of the year. The date of the disappearance of the continuous and seasonally permanent snow pack (S_{stop}) was defined as the first day of the calendar year where the snow depth is 0 cm. The date where the snow pack starts to melt until its disappearance (S_{melt}) was the first day, between the date of the maximum snow height recorded (often in March) and S_{stop}, for which the variation of snow height between two consecutive days would be negative for at least five consecutive days. Concretely, we set all the winter precipitations to 0 mm and released their sum at the period of snow-melt. That is to say: for each winter, between S_{start} and S_{melt} daily precipitation was set up to 0 mm while between S_{melt} and S_{stop} daily precipitation (P) was set up to $\frac{1}{S_{stop}-S_{melt}} \times \sum_{S_{start}}^{S_{stop}} P$. The validity of these empirical definitions was graphically verified (Fig. B.2).

B.3 Additionnal results

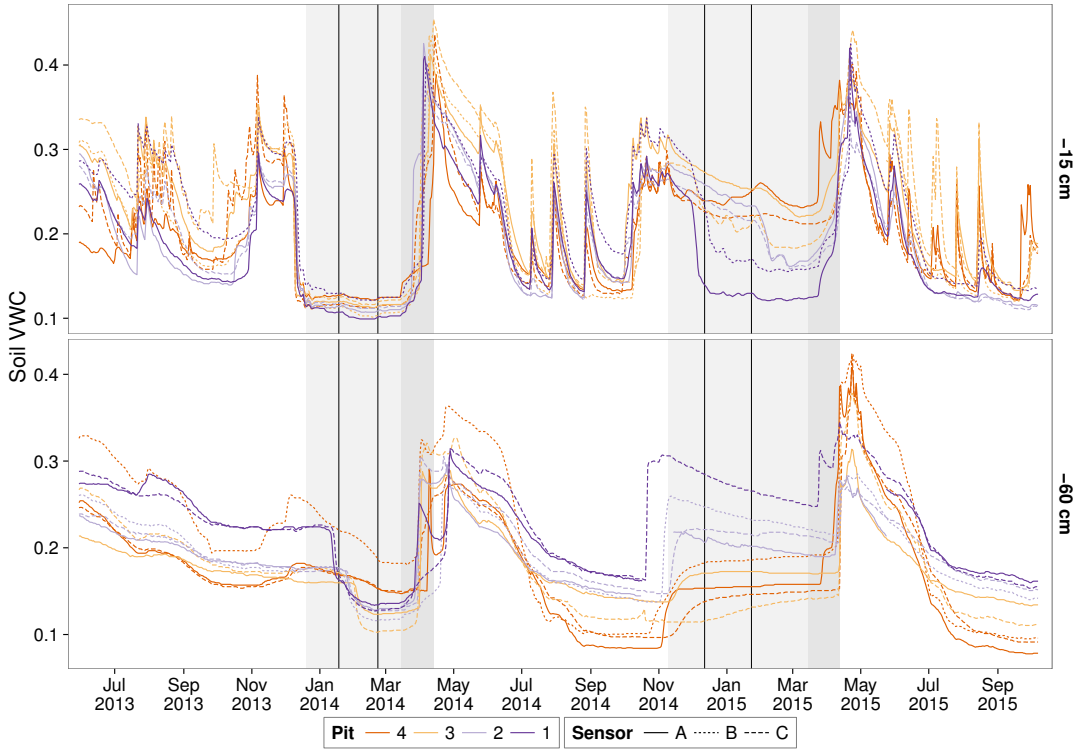


Figure B.3: Variability of the soil volumetric water content (VWC) measured at BAR aspen forest. Daily average per sensor. Four soil pits were set up with 2–3 VWC sensors at −15 cm and −60 cm. VWC measured under the control snow treatment are displayed in purple while VWC measured under the increased snow treatment are displayed in orange. The snow season is highlighted in grey and the snow-melt in dark grey.

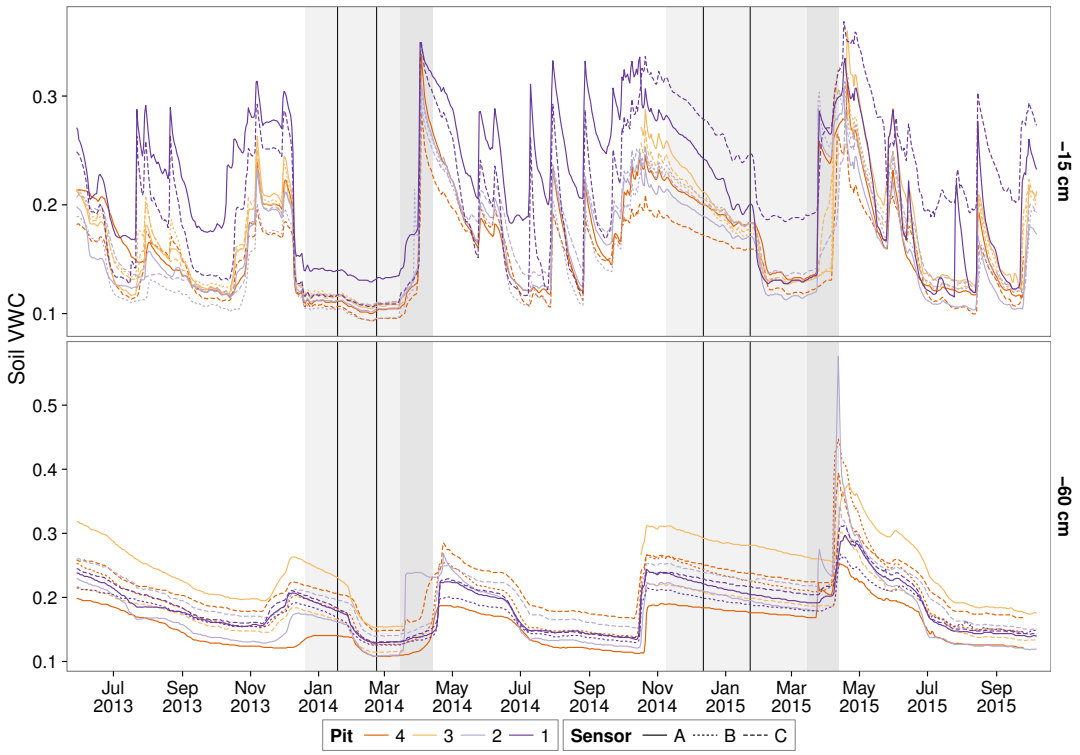


Figure B.4: Variability of the soil volumetric water content (VWC) measured at BAR grassland. Daily average per sensor. Four soil pits were set up with 2–3 VWC sensors at −15 cm and −60 cm. VWC measured under the control snow treatment are displayed in purple while VWC measured under the increased snow treatment are displayed in orange. The snow season is highlighted in grey and the snow-melt in dark grey.

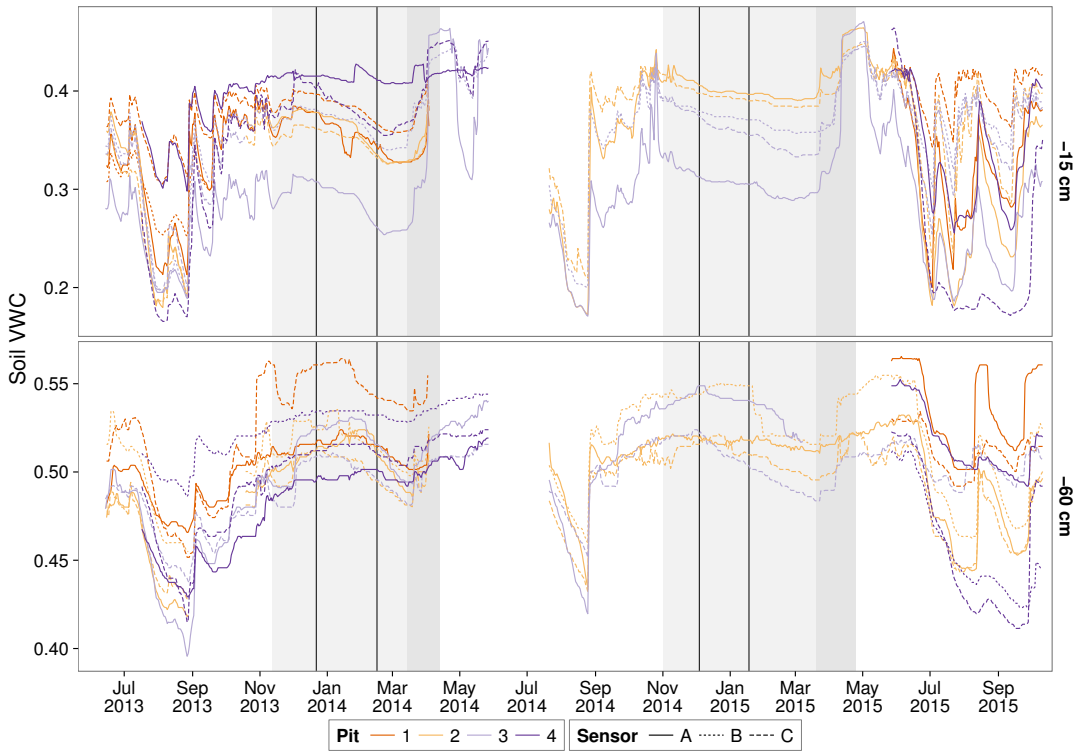


Figure B.5: Variability of the soil volumetric water content (VWC) measured at TOM aspen forest. Daily average per sensor. Four soil pits were set up with 2–3 VWC sensors at −15 cm and −60 cm. VWC measured under the control snow treatment are displayed in purple while VWC measured under the increased snow treatment are displayed in orange. The snow season is highlighted in grey and the snow-melt in dark grey.

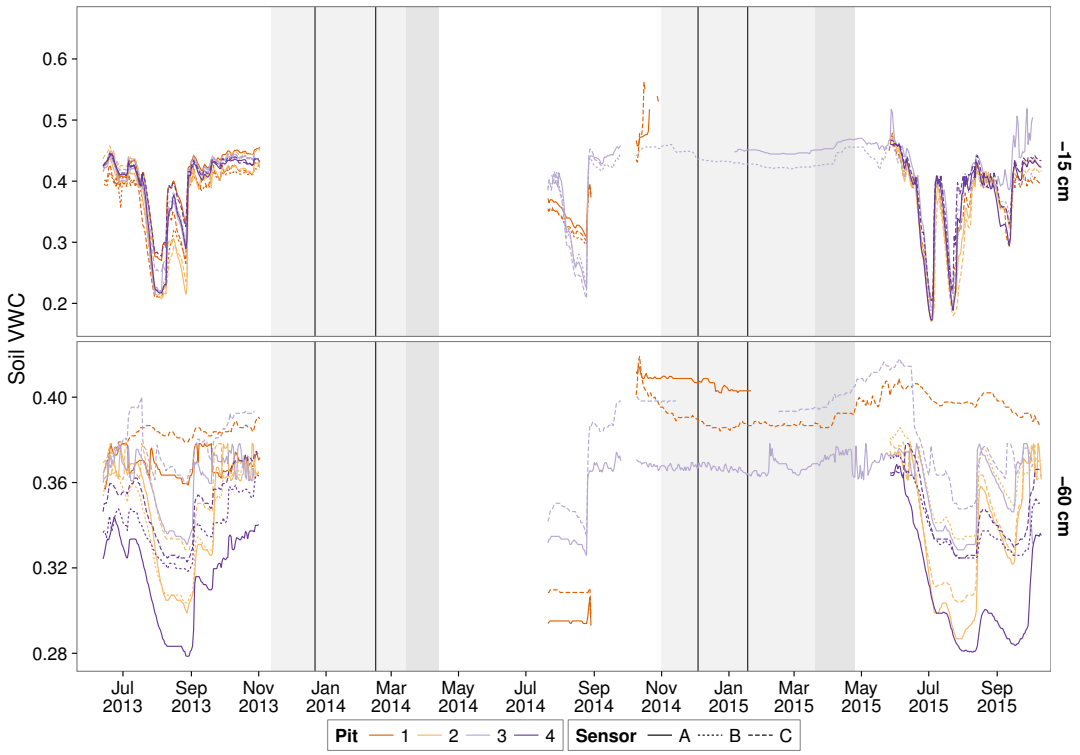


Figure B.6: Variability of the soil volumetric water content (VWC) measured at TOM grassland. Daily average per sensor. Four soil pits were set up with 2–3 VWC sensors at −15 cm and −60 cm. VWC measured under the control snow treatment are displayed in purple while VWC measured under the increased snow treatment are displayed in orange. The snow season is highlighted in grey and the snow-melt in dark grey.

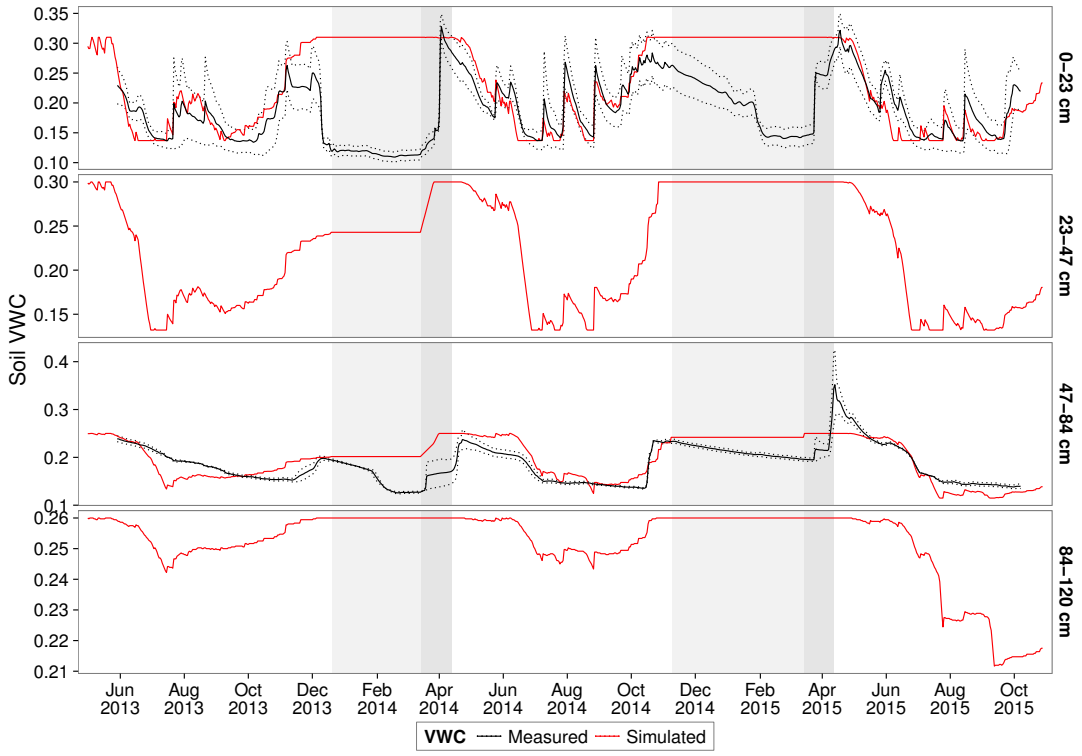


Figure B.7: Volumetric water content (VWC, in $m^3\ m^{-3}$) in four soil layers at BAR grassland: simulation with the model BILJOU (red line) and field measurements (black line) over the period of VWC monitoring. The black dotted lines indicate the minimum and the maximum of the mean VWC (mean of 2–3 sensors per depth and per pit) measured on 1–2 plots. The snow season is highlighted in grey and the snow-melt in dark grey. In winter, when the soil temperature is close to or below 0 °C, the soil moisture sensors do not always provide accurate data.

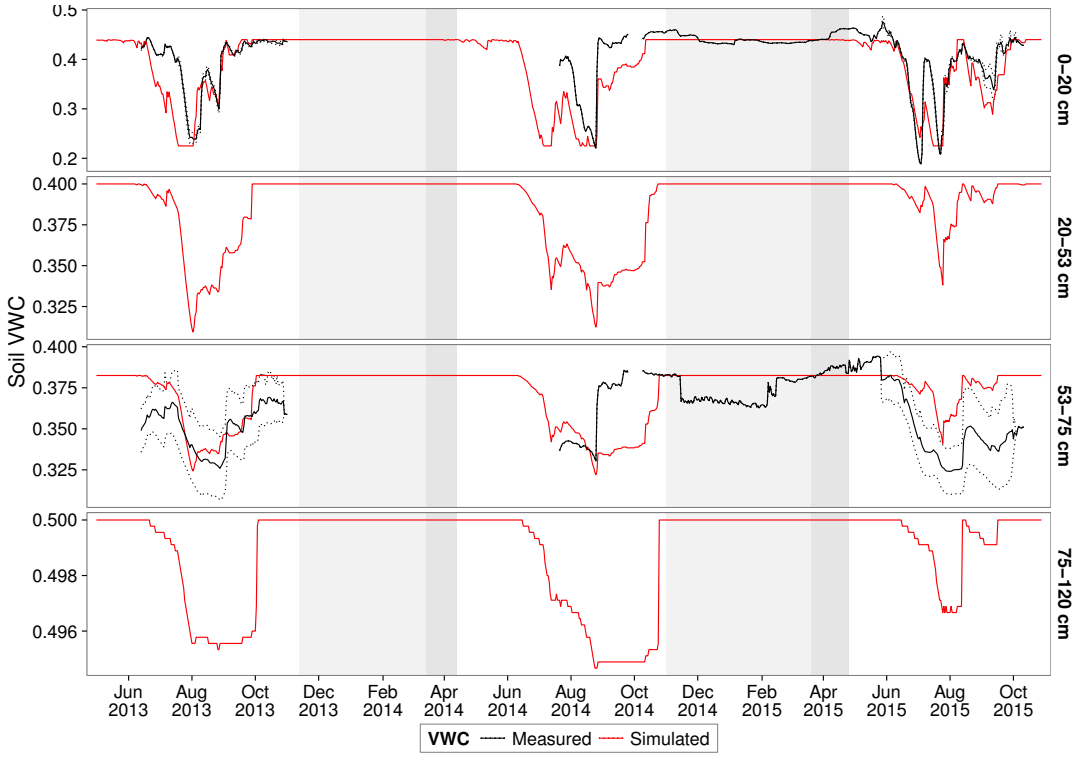


Figure B.8: Volumetric water content (VWC, in $m^3\ m^{-3}$) in four soil layers at TOM grassland: simulation with the model BILJOU (red line) and field measurements (black line) over the period of VWC monitoring. The black dotted lines indicate the minimum and the maximum of the mean VWC (mean of 2–3 sensors per depth and per pit) measured on 1–2 plots. The snow season is highlighted in grey and the snow-melt in dark grey. In winter, when the soil temperature is close to or below 0 °C, the soil moisture sensors do not always provide accurate data.

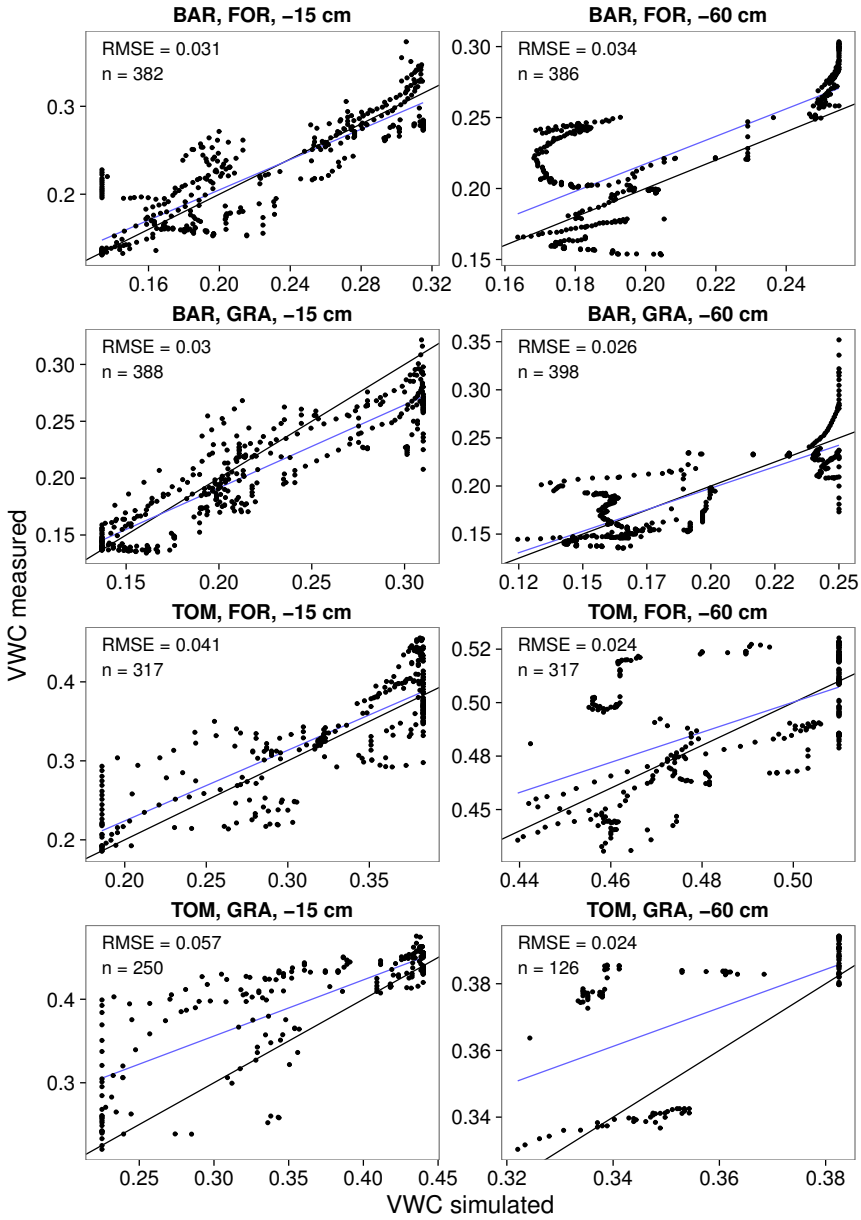


Figure B.9: Quality of the calibration of the water budget model BILJOU for BAR and TOM aspen forest (FOR) and grassland (GRA). The soil volumetric water content (VWC) measured is plotted against the soil VWC simulated, excluding the snow period (where the simulation is artificially maintained to a constant value) and the VWC measured when soil temperature is $< 0\,^{\circ}C$ (measurements may not be accurate below this threshold). The 1:1 line is represented in black. The blue line is a simple linear relation between y and x axes. The root mean square error (RMSE) and the number of points considered (n) are displayed.

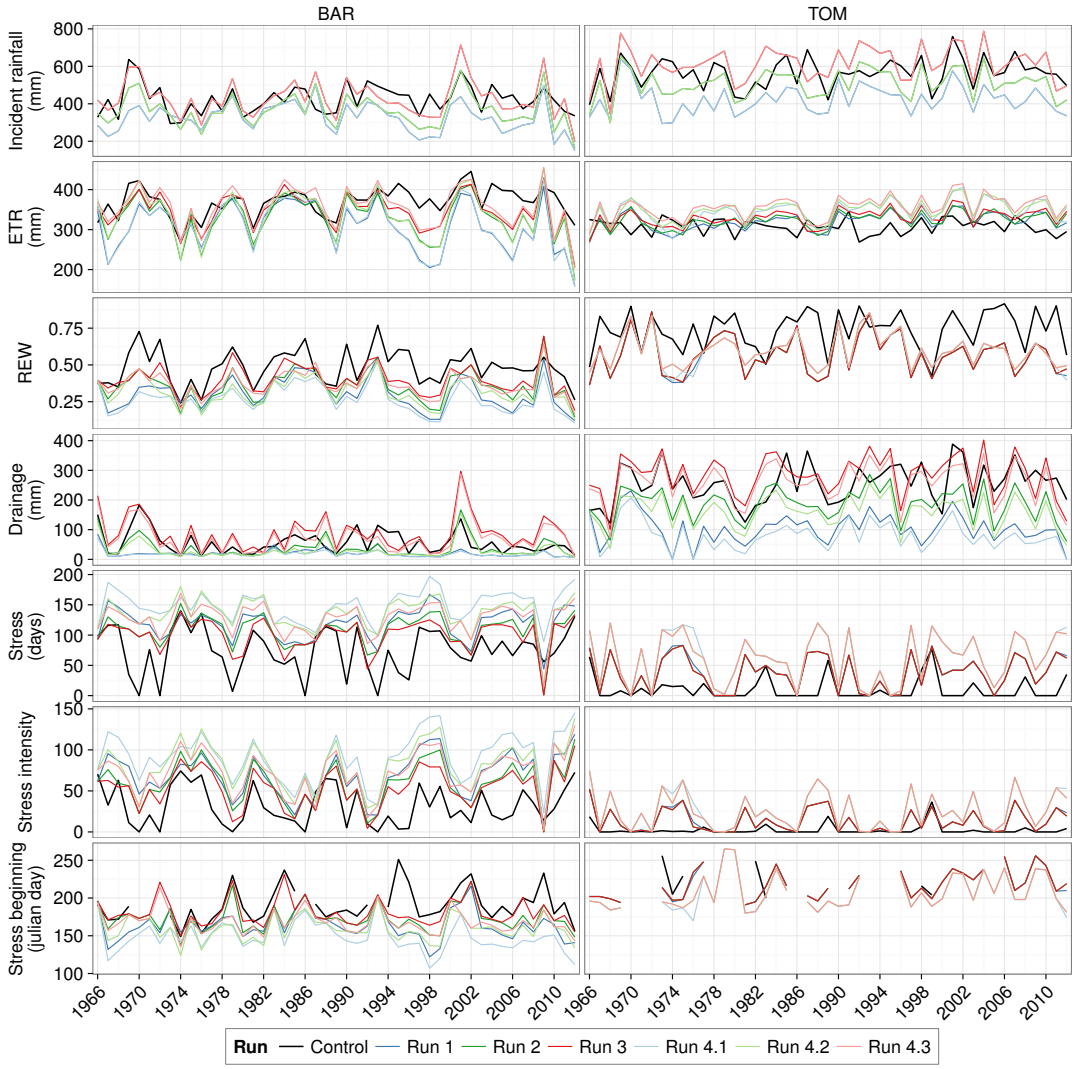


Figure B.10: Yearly averaged chronology of water budget simulations in BAR and TOM aspen forest. For each year, daily incident rainfall, stress and drainage were summed while daily REW was averaged over the 15 days time step.

Appendix C

Distributions of fine root length and mass with soil depth in natural ecosystems of south-western Siberia

Table C.1: Results of all the one-way ANOVA testing a site effect.

Test on	Veg. Cover	Species	Diameter	F	df	p	sig.[a]
Roots bottom pit	Forest	overall	coarse	4.5922	5	0.01424	*
		overall	fine	3.5211	5	0.03435	*
	Grassland	overall	coarse	0.7514	4	0.5793	
		overall	fine	1.4598	4	0.2852	
FRL in litter	Forest	overall	< 0.8	1.6188	5	0.2287	
		aspen	< 0.8	2.6003	5	0.08126	.
		non-aspen	< 0.8	1.915	5	0.1654	
	Grassland	overall	< 0.8	3.3321	4	0.05582	.
FRM in litter	Forest	overall	< 0.8	1.3484	5	0.3096	
		aspen	< 0.8	1.5792	5	0.239	
		non-aspen	< 0.8	2.1616	5	0.1272	
	Grassland	overall	< 0.8	1.9599	4	0.1317	
beta FRL	Forest	overall	< 0.8	8.4154	5	0.001276	**
		aspen	< 0.8	1.8589	5	0.1757	
		non-aspen	< 0.8	2.2469	5	0.1223	
	Grassland	overall	< 0.8	2.7179	4	0.091	.
Total FRL	Forest	overall	< 0.8	4.8921	5	0.01135	*
		aspen	< 0.8	7.3919	5	0.002233	**
		non-aspen	< 0.8	2.0074	5	0.1497	
	Grassland	overall	< 0.8	12.21	4	0.00073	***
FRL top 30 cm	Forest	overall	< 0.8	7.5791	5	0.002008	**
		aspen	< 0.8	2.8304	5	0.06488	.
		non-aspen	< 0.8	2.1838	5	0.1302	
	Grassland	overall	< 0.8	3.8992	4	0.03683	*
beta FRM	Forest	overall	< 0.8	3.5493	5	0.03351	*
		aspen	< 0.8	3.6112	5	0.03175	*
		non-aspen	< 0.8	1.4347	5	0.2864	
	Grassland	overall	< 0.8	1.5297	4	0.2663	
Total FRM	Forest	overall	< 0.8	4.7124	5	0.01299	*
		aspen	< 0.8	3.7766	5	0.02754	*
		non-aspen	< 0.8	2.3462	5	0.105	
	Grassland	overall	< 0.8	8.1198	4	0.003487	**
FRM top 30 cm	Forest	overall	< 0.8	4.7898	5	0.01225	*
		aspen	< 0.8	7.0496	5	0.002725	**
		non-aspen	< 0.8	1.8805	5	0.1778	
	Grassland	overall	< 0.8	1.7126	4	0.2232	

[a]Significance levels: "***" $p < 0.001$; "**" $p < 0.01$; "*" $p < 0.05$; "." $p < 0.1$.

Table C.2: Length and mass of fine roots of a diameter < 0.8 mm in the litter layer. Mean of 3 replicates per site ± standard error of the mean. Different letters denote significant differences at $p < 0.05$ level using a Tukey post-hoc comparison. ANOVA results are given in C.1.

			FRL ($m\,m^{-2}$)			FRM ($g\,m^{-2}$)		
Veg. Cover	Species	Site	mean	se	stat	mean	se	stat
Forest	Overall	FS1	17.81	5.46	a	1.04	0.34	a
		FS2	38.87	19.15	a	4.80	3.40	a
		FS3	31.87	3.84	a	2.85	0.54	a
		FS4	23.20	9.58	a	1.12	0.72	a
		ST1	11.50	3.16	a	0.49	0.16	a
		ST2	8.23	2.55	a	0.63	0.33	a
	Aspen	FS1	1.66	1.66	a	0.18	0.18	a
		FS2	21.67	11.90	a	3.29	2.42	a
		FS3	2.12	1.06	a	0.39	0.22	a
		FS4	4.15	3.46	a	0.35	0.30	a
		ST1	0.74	0.25	a	0.23	0.11	a
		ST2	0.00	0.00	a	0.00	0.00	a
	Non-aspen	FS1	16.15	4.62	a	0.87	0.28	a
		FS2	17.20	8.74	a	1.51	1.02	a
		FS3	29.75	4.60	a	2.46	0.56	a
		FS4	19.05	6.58	a	0.77	0.44	a
		ST1	10.76	2.95	a	0.26	0.05	a
		ST2	8.23	2.55	a	0.63	0.33	a
Grassland	Overall	FS1	5.13	3.34	a	0.11	0.09	a
		FS2	0.89	0.89	a	0.06	0.06	a
		FS3	15.93	9.90	a	0.29	0.18	a
		FS4	18.68	1.57	a	0.44	0.20	a
		ST2	0.00	0.00	a	0.00	0.00	a

Table C.3: Structure of the total fine root length calculated over 120 cm. Mean and standard error of the mean of 3 pits per site. Results are expressed in % of total FRL, diameters are in mm.

			FS1		FS2		FS3		FS4		ST1		ST2	
Veg.	Species	Diameter	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Forest	Aspen	overall	78.44	14.00	31.51	4.50	65.63	8.21	37.13	10.84	54.08	11.35	52.16	8.57
	Non-aspen	overall	21.56	14.00	68.49	4.50	34.37	8.21	62.87	10.84	45.92	11.35	47.84	8.57
	Overall	overall	100.00		100.00		100.00		100.00		100.00		100.00	
	Aspen	< 0.2	58.44	1.16	68.13	5.98	70.42	5.30	66.68	6.46	49.50	6.66	61.29	4.06
		0.2-0.4	26.69	1.42	24.27	6.20	17.87	4.07	25.61	6.09	38.02	5.66	29.50	3.05
		0.4-0.8	11.00	1.81	6.18	1.03	9.64	1.91	6.48	1.97	6.95	0.84	8.09	2.87
		0.8-1.2	3.65	2.15	1.41	0.77	1.86	0.41	0.80	0.80	5.52	2.80	0.43	0.43
		1.2-2.0	0.22	0.22	0.00	0.00	0.21	0.21	0.43	0.43	0.00	0.00	0.68	0.68
		overall	100.00		100.00		100.00		100.00		100.00		100.00	
	Non-aspen	< 0.2	86.63	10.17	78.01	8.95	88.52	4.95	89.62	2.99	69.10	17.00	67.94	17.12
		0.2-0.4	12.98	10.30	11.33	3.52	11.44	4.95	9.52	3.56	16.35	9.16	24.79	16.98
		0.4-0.8	0.14	0.14	6.33	1.52	0.04	0.04	0.63	0.46	10.32	5.21	7.27	4.77
		0.8-1.2	0.25	0.25	2.67	2.59	0.00	0.00	0.24	0.24	4.23	4.23	0.00	0.00
		1.2-2.0	0.00	0.00	1.66	1.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		overall	100.00		100.00		100.00		100.00		100.00		100.00	
	Overall	< 0.2	65.71	5.72	74.40	7.72	77.96	1.39	81.75	4.63	54.22	7.18	61.22	7.86
		0.2-0.4	22.47	4.06	15.69	4.21	14.56	2.01	14.47	3.90	30.02	5.26	30.54	7.74
		0.4-0.8	9.20	2.72	6.22	1.31	6.10	0.96	3.06	1.15	9.24	1.87	7.71	3.65
		0.8-1.2	2.41	1.25	2.45	1.69	1.21	0.29	0.53	0.29	6.52	1.15	0.28	0.28
		1.2-2.0	0.21	0.21	1.24	1.24	0.17	0.17	0.18	0.18	0.00	0.00	0.24	0.24
		overall	100.00		100.00		100.00		100.00		100.00		100.00	
Grassland	Overall	< 0.2	90.12	2.48	91.42	2.40	80.64	1.00	81.24	0.24			87.01	2.48
		0.2-0.4	7.81	1.28	6.94	1.65	17.35	1.86	15.53	0.99			9.61	2.63
		0.4-0.8	1.51	0.93	0.88	0.28	1.43	0.73	2.64	0.86			2.36	0.93
		0.8-1.2	0.56	0.35	0.76	0.50	0.58	0.42	0.50	0.25			1.02	0.83
		1.2-2.0	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.09			0.00	0.00
		overall	100.00		100.00		100.00		100.00				100.00	

Table C.4: Structure of the total fine root mass calculated over 120 cm. Mean and standard error of the mean of 3 pits per site. Results are expressed in % of total FRM, diameters are in mm.

			FS1		FS2		FS3		FS4		ST1		ST2	
Veg.	Species	Diameter	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Forest	Aspen	overall	86.08	9.95	36.95	12.89	83.18	4.07	52.80	12.15	62.75	22.48	70.13	8.53
	Non-aspen	overall	13.92	9.95	63.05	12.89	16.82	4.07	47.20	12.15	37.25	22.48	29.87	8.53
	Overall	overall	100.00		100.00		100.00		100.00		100.00		100.00	
	Aspen	< 0.8	78.95	12.90	85.87	7.29	74.91	2.02	89.05	10.95	79.58	10.87	81.06	10.1
		0.8-2	21.05	12.90	14.13	7.29	25.09	2.02	10.95	10.95	20.42	10.87	18.94	10.1
		overall	100.00		100.00		100.00		100.00		100.00		100.00	
	Non-aspen	< 0.8	96.63	3.37	74.67	21.58	100.00	0.00	86.75	11.60	76.41	23.59	100	0
		0.8-2	3.37	3.37	25.33	21.58	0.00	0.00	13.25	11.60	23.59	23.59	0	0
		overall	100.00		100.00		100.00		100.00		100.00		100.00	
	Overall	< 0.8	83.21	9.51	71.45	16.17	78.97	2.78	89.62	5.92	63.11	11.26	86.11	8.44
		0.8-2	16.79	9.51	28.55	16.17	21.03	2.78	10.38	5.92	36.89	11.26	13.89	8.44
		overall	100.00		100.00		100.00		100.00		100.00		100.00	
Grassland	Overall	< 0.8	93.45	4.26	90.47	4.86	83.97	11.64	87.73	6.14			77.92	18.09
		0.8-2	6.55	4.26	9.53	4.86	16.03	11.64	12.27	6.14			22.08	18.09
		overall	100.00		100.00		100.00		100.00				100.00	

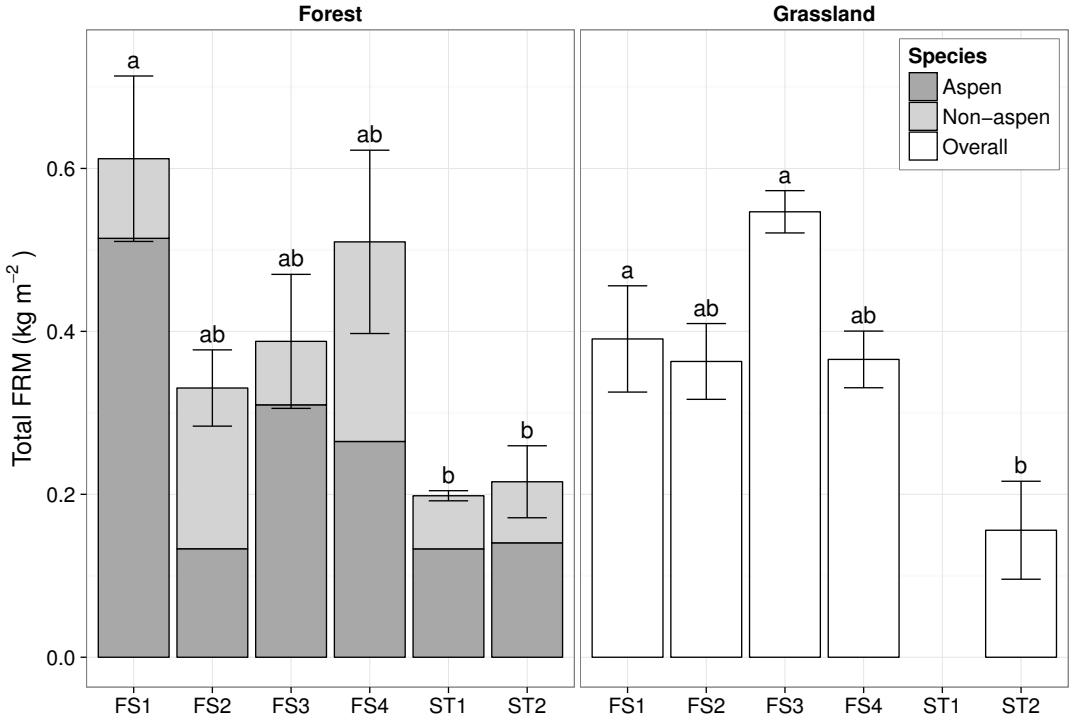


Figure C.1: Total fine root mass over 120 cm in forest (left panel) and grassland (right panel). Mean and standard error of the mean of 3 replicates per site. In forest, total fine root mass is detailed for aspen (dark grey) and non-aspen (light grey). Results presented for roots with a diameter < 0.8 mm. Different letters denote significant differences at $p < 0.05$ level using a Tukey post-hoc comparison. ANOVA results are given in Table C.1

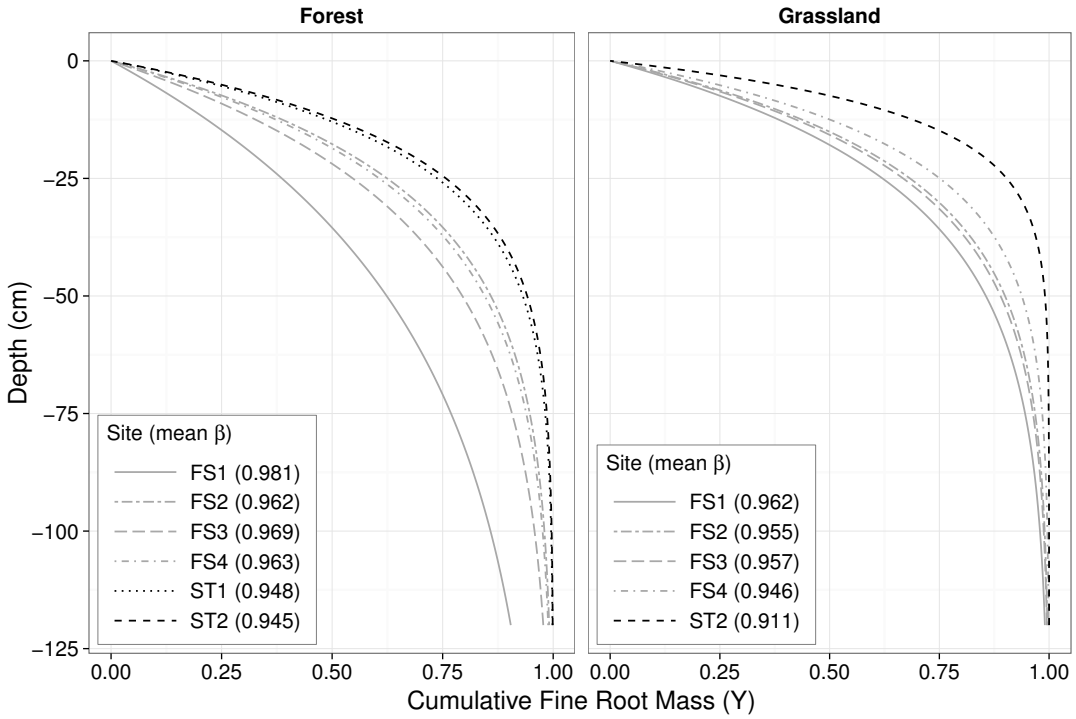


Figure C.2: Cumulative fine root mass (cumulative proportion) as a function of soil depth in forest (left panel) and grassland (right panel) for the six sites. The figure shows the differences between sites. Species are not sorted, diameter < 0.8 mm. The line was generated with the mean β (of 3 pits) from Eq. 5.5: $Y = 1 - \beta^d$ (Gale and Grigal 1987).

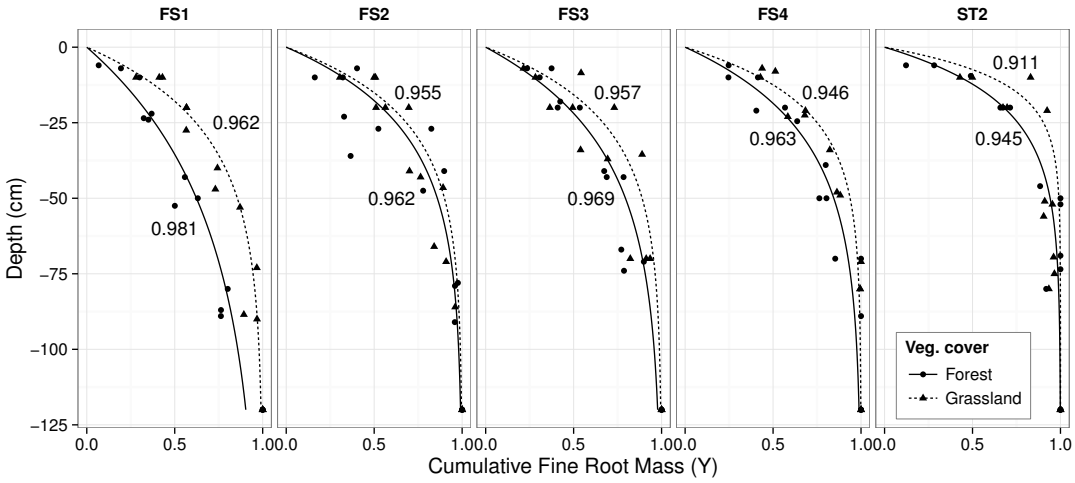


Figure C.3: Cumulative fine root mass (cumulative proportion) as a function of soil depth in forest and grassland for the six sites. The figure shows the differences between forest and grassland within sites and the quality of model fitting. Species are not sorted, diameter < 0.8 mm. Points are field measurements (3 per site and depth) and line was generated with the mean β (of 3 pits) from Eq. 5.5: $Y = 1 - \beta^d$ (Gale and Grigal 1987).

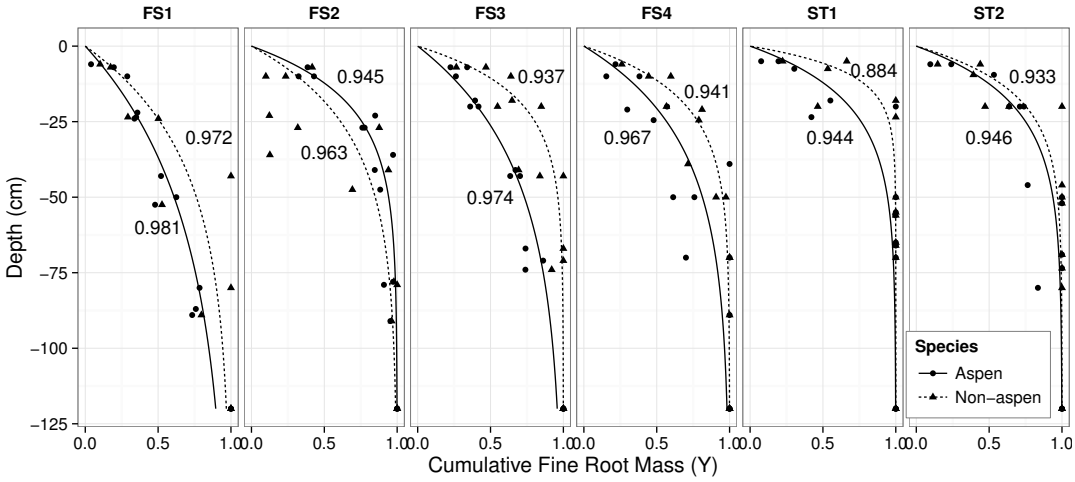


Figure C.4: Cumulative fine root mass (cumulative proportion) as a function of soil depth in forest for the six sites. The figure shows the differences between aspen and non-aspen fine root systems within forest sites and the quality of model fitting. Aspen and non-aspen (understorey vegetation) are sorted, diameter < 0.8 mm. Points are field measurements (3 per site and depth) and line was generated with the mean β (of 3 pits) from Eq. 5.5: $Y = 1 - \beta^d$ (Gale and Grigal 1987).

Appendix D

What is the P value of Siberian soils?

Table D.1: Detailed climatic features of the study sites. Data averaged on the period 1981–2010. The data presented for each site come from the closest weather stations.

Variable	Period	BAR	CHE	KRA	SAE	SAW	TOM
WMO index of the station		29838	29539	29915	29745	29736	29430
Distance site–station (km)		4	28	76	18	64	38
Air Temperature (°C)	MAT	2.7	1.3	2.9	2.3	1.2	0.9
	DJF	-14.1	-15.2	-15.1	-15.4	-17.6	-15.6
	MAM	3.4	2.0	3.4	3.4	2.8	1.6
	JJA	18.3	17.0	19.7	17.4	16.9	16.7
	SON	2.8	1.2	3.2	3.0	2.2	0.8
Precipitation (mm)	MAP	431.5	509.8	324.5	432.3	453.0	566.5
	DJF	69.8	84.5	53.2	54.3	66.1	104.7
	MAM	85.1	91.3	58.2	78.9	75.1	98.2
	JJA	166.6	184.8	135.3	182.2	168.8	202.9
	SON	107.7	146.4	76.1	106.1	115.9	157.2
Snow Height (cm)	climax	48.8	42.5	18.8	38.0	54.3	70.6
SCD 1 cm (days)	year	157.2	167.6	141.9	144.5	149.5	178.1
SCD 20 cm (days)	year	108.3	118.3	25.2	88.3	116.4	145.5
Soil Temp. at 20 cm (°C)	DJF	-1.5		-6.0			-0.4
	MAM	4.3		4.0			2.4
	JJA	18.9		20.3			16.4
	SON	6.5		7.3			5.8
Soil frozen at 20 cm (days)	year	86.8		130.1			44.5
Depth of soil frozen (m)	DJF	20–40		40–80			0–20

WMO: World Meteorological Organization; MAT: mean annual temperature;
MAP: mean annual precipitations; SCD: snow cover duration;
D, J, F, M, A, M, J, J, A, S, O and N are the months of the year
climax: maximum snow depth, i.e. mean between mid-February and mid-March

Table D.2: Detailed forest stand characteristics. Mean and standard error of the mean for 3 plots per site.

	BAR		CHE		KRA		SAE		SAW		TOM	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Surface described (m^2)[a]	100–325	—	800–1050	—	242–696	—	156–192	—	240–350	—	264–420	—
Density (tree/ha)	1664.0	271.9	387.3	39.5	767.0	235.4	1882.7	145.8	1144.0	147.1	1139.3	188.8
% aspen in density[b]	92.6	—	93.2	—	98.0	—	100.0	—	95.5	—	86.0	—
Basal Area ($m^2\ ha^{-1}$)	34.4	8.7	36.4	3.5	42.6	6.8	29.1	1.9	47.5	7.1	43.8	7.6
% aspen in basal area[b]	90.4	—	89.9	—	97.9	—	100.0	—	97.5	—	95.9	—
DBH (cm)	14.9	1.1	33.9	0.2	26.3	2.3	13.7	0.8	22.8	0.8	21.4	2.6
Height (m)	11.2	0.3	28.0	1.7	18.7	1.5	15.7	0.1	24.8	1.1	18.2	2.1
Age (years)	26.9	1.3	61.7	3.4	51.0	2.6	21.4	3.8	46.7	1.3	55.8	14.1
LAI (m^2 leaves m^{-2} soil)	4.9	0.6	3.8	0.3	3.8	0.3	5.1	0.6	5.0	0.4	2.9	0.5

Only pole and tree stages are included here (i.e. diameter at 1.3 m > 7 cm and height > 1.3 m). DBH: Diameter at breast height; LAI: Leaf area index.

[a]Surface area described, plot set to include at least 30 *Populus tremula*

[b]Other tree species: mostly *Betula pendula* but also, very rarely, *Abies sibirica*, *Padus avium*, *Pinus sibirica* and *Pinus sylvestris*

Table D.3: Composition of the understorey vegetation in forest (herbaceous, shrub and tree species with a height < 1.3 m and a diameter < 1 cm) and herbaceous species in grassland. Range of the number of species over 3 replicates and dominant species.

Site	n[a]	Dominant species[b]
Forest		
BAR	14–18	*Populus tremula* L., *Heracleum sibiricum* L.
CHE	21–27	*Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth
SAE	20–44	*Populus tremula* L., *Carex pallescens* L., *Phlomis tuberosa* L.
SAW	11–17	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth, *Urtica dioica* L.
TOM	16–29	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth
Grassland		
BAR	13–17	*Bromopsis inermis* (Leys.) Holub, *Cuscuta europaea* L., *Festuca pseudovina* Hack. ex Wiesb.
CHE	19–26	*Bromopsis inermis* (Leys.) Holub, *Alopecurus pratensis* L.
SAE	22–60	*Bromopsis inermis* (Leys.) Holub, *Seseli ledebourii* G. Don fil., *Filipendula vulgaris* Moench
TOM	20–21	*Calamagrostis epigeios* (L.) Roth, *Bromopsis inermis* (Leys.) Holub, *Alopecurus pratensis* L.

[a]number of species; [b]we retained species occurring in at least 2 of the 3 site replicates and with a mean score on the Braun-Blanquet scale > 1

Table D.4: Litter and soil horizons description and their main physico-chemical properties. "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands) i.e. mainly OL and OF horizons, and possibly OH (at BAR, CHE, KRA and SAE) at the date of sampling.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
Horizon type*											
−5	AU	AU	O	AU	AY	AY	AU	AU	AU	Ad	AY
−15	AU	AU_e	AU	AU	AEL	AEL	AU	AU_e	AU	AU	AEL
−30	BEL	BEL	AU	B	EL	AEL	AU	EL	AU	B	BEL_g
−60	B	BT	BEL	B	BEL	BEL_g	B	BT	B_{Ca}	BC_{Ca}	BT_g
−100	BT	BT	BM	M	BT	BT_g	B_{Ca}	BT	B_{Ca}	M	BT_g
Thickness* (cm)											
−5	7.7	9.0	8.0	8.7	5.8	7.2	10.0	10.0	8.5	8.3	10.0
−15	15.5	16.7	11.3	13.2	14.7	12.8	12.5	10.0	11.5	13.8	10.3
−30	25.3	15.8	23.0	24.5	33.2	29.3	24.2	23.5	15.5	21.5	32.7
−60	36.8	41.2	28.3	30.0	13.3	24.8	37.2	30.8	34.5	33.3	21.8
−100	34.7	37.3	49.3	43.7	53.0	45.8	36.2	45.7	50.0	43.0	45.2
Litter mass* ($kg\,m^{-2}$)											
	2.96	2.43	4.29	1.98	0.94	1.15	0.71	0.20	2.29	0.88	0.21
Density*											
−5	1.0	0.8	0.7	0.5	0.7	0.9	1.0	1.0	0.9	0.9	0.9
−15	1.2	1.0	1.0	0.8	1.0	1.1	1.3	1.1	1.0	1.1	1.2
−30	1.2	1.2	1.2	1.1	1.3	1.2	1.3	1.1	1.2	1.3	1.3
−60	1.3	1.4	1.4	1.3	1.5	1.5	1.7	1.4	1.4	1.3	1.5
−100	1.4	1.5	1.6	1.1	1.6	1.4	1.7	1.4	1.5	1.4	1.4

*: mean of 3 replicates

Table D.4: Continued.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
Granulometry 0–2 µm (%)											
−5	27.7	22.8	32.5	40.7	22.2	23.2	27.5	25.5	38.4	35.3	22.0
−15	27.2	18.6	29.6	36.8	20.4	21.9	27.7	25.1	36.1	34.9	21.2
−30	26.8	18.6	29.9	31.4	18.2	19.7	26.2	23.1	30.9	24.5	20.5
−60	26.1	31.5	32.9	17.3	23.1	31.1	25.6	30.8	28.7	14.8	37.8
−100	25.3	28.4	23.6	8.0	31.2	40.8	25.3	27.8	26.4	6.5	38.6
Granulometry 2–20 µm (%)											
−5	23.2	36.2	17.4	26.5	37.9	38.8	20.7	34.4	21.1	23.8	38.9
−15	23.0	37.0	15.3	25.3	38.2	38.7	21.0	34.7	7.3	23.9	40.5
−30	22.8	36.2	14.9	25.1	38.3	39.1	19.5	34.9	23.7	19.2	40.1
−60	23.4	27.6	14.6	13.2	36.2	32.6	22.7	27.2	15.7	11.2	30.3
−100	21.9	28.3	12.0	5.5	31.5	30.6	16.1	27.6	17.2	5.6	32.1
Granulometry 20–50 µm (%)											
−5	35.3	32.8	14.5	14.9	34.4	30.2	35.5	32.3	15.3	17.0	30.8
−15	35.7	34.9	14.8	15.6	36.6	31.0	32.7	32.0	27.3	17.6	31.7
−30	35.2	34.8	14.2	15.2	37.5	31.3	34.8	33.7	16.5	15.3	30.8
−60	37.3	31.5	13.5	8.8	35.4	27.4	33.7	31.7	16.3	8.7	25.7
−100	39.8	32.9	16.0	3.4	32.7	24.6	34.4	34.1	17.3	3.1	25.6
Granulometry 50–200 µm (%)											
−5	13.0	7.2	25.1	4.4	4.6	6.9	14.0	7.3	17.3	4.7	6.7
−15	13.5	8.3	26.5	5.2	3.9	7.4	16.0	7.7	21.2	4.2	4.7
−30	14.5	8.7	26.3	5.7	5.2	8.8	15.3	7.8	19.1	3.3	6.6
−60	12.2	8.4	24.2	5.3	4.3	7.7	12.8	9.7	24.0	4.5	5.4
−100	12.0	8.3	27.1	4.5	4.1	3.5	19.8	10.1	20.5	6.6	3.1

*: mean of 3 replicates

Table D.4: Continued.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
Granulometry 200–2000 µm (%)											
−5	0.7	0.9	10.4	13.4	0.8	0.8	2.2	0.4	7.8	19.1	1.5
−15	0.5	1.1	13.7	17.0	0.8	0.9	2.5	0.4	8.0	19.3	1.8
−30	0.6	1.6	14.6	22.5	0.7	1.0	2.5	0.4	7.8	37.6	1.9
−60	0.9	0.9	13.5	55.2	0.9	1.1	1.8	0.5	7.9	60.1	0.7
−100	0.9	0.8	9.7	73.7	0.4	0.4	4.3	0.3	7.0	76.7	0.4
pH											
Litter	6.81	6.81	7.27	6.86	6.86	6.59	6.65	6.36	6.79	6.86	6.31
−5	6.10	5.73	6.86	6.17	6.07	5.37	6.50	5.95	7.16	6.47	5.45
−15	6.12	5.40	6.34	5.97	5.45	5.25	7.20	6.27	7.80	6.58	5.54
−30	6.52	5.67	6.32	6.15	5.25	5.25	7.73	6.29	8.30	7.28	5.63
−60	6.34	6.18	7.99	7.09	5.39	5.60	7.88	6.41	9.10	8.12	6.02
−100	6.34	7.60	8.52	8.36	5.70	6.53	8.00	6.43	8.95	8.55	7.32
Organic C ($g\,kg^{-1}$)											
Litter	305.00	377.00	398.00	362.00	341.00	400.00	370.00	338.00	202.00	290.00	368.00
−5	39.20	53.00	54.30	113.00	52.90	37.20	35.30	40.30	68.10	51.20	32.50
−15	32.80	22.40	34.90	63.60	25.00	24.80	29.10	35.40	42.80	46.10	21.30
−30	28.60	10.70	25.00	16.90	13.10	13.90	18.20	28.50	30.80	6.79	10.70
−60	8.05	3.68	6.79	3.07	4.92	5.49	5.71	4.35	12.80	2.86	3.76
−100	2.73	2.43	3.68	1.26	2.43	2.99	2.79	2.68	3.07	1.11	2.33
Total N ($g\,kg^{-1}$)											
Litter	12.70	12.00	14.50	16.70	13.80	11.10	15.50	12.20	11.50	14.90	10.70
−5	2.91	3.48	4.10	8.53	4.22	2.92	2.83	2.80	5.32	3.90	2.65
−15	2.44	1.47	2.57	4.65	2.14	2.09	2.31	2.40	3.23	3.47	1.77
−30	2.09	0.75	1.85	1.21	1.15	1.17	1.45	1.89	2.34	0.48	0.85
−60	0.65	0.36	0.58	0.26	0.45	0.50	0.51	0.38	1.01	0.22	0.40
−100	0.26	0.25	0.31	0.09	0.29	0.36	0.21	0.27	0.24	0.10	0.29

*: mean of 3 replicates

Table D.4: Continued.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
C:N											
Litter	24.00	31.50	27.50	21.70	24.70	36.10	23.90	27.60	17.50	19.40	34.40
−5	13.50	15.20	13.30	13.30	12.50	12.70	12.50	14.40	12.80	13.10	12.30
−15	13.50	15.20	13.60	13.70	11.70	11.90	12.60	14.70	13.20	13.30	12.10
−30	13.70	14.40	13.50	13.90	11.40	11.90	12.60	15.10	13.10	14.10	12.70
−60	12.40	10.30	11.70	11.90	11.00	11.10	11.20	11.30	12.70	12.80	9.38
−100	10.40	9.55	11.90	14.50	8.27	8.42	13.10	9.78	12.60	11.00	8.05
C:P											
Litter	246.84	320.99	301.84	294.01	225.07	395.33	317.39	252.16	180.02	219.93	386.09
−5	38.53	62.25	74.47	103.11	50.91	48.97	40.22	42.15	80.40	55.58	46.81
−15	34.46	33.75	56.69	70.03	28.92	36.65	33.66	37.71	61.27	52.79	34.11
−30	29.77	17.02	46.18	40.62	17.05	24.87	24.09	31.69	48.99	12.06	20.25
−60	10.54	5.44	17.20	9.49	8.41	11.23	9.62	6.31	24.84	4.68	7.62
−100	4.28	3.69	9.01	3.95	3.76	5.66	4.70	3.86	7.41	1.87	4.34
N:P											
Litter	10.28	10.22	11.00	13.56	9.11	10.97	13.30	9.10	10.25	11.30	11.23
−5	2.86	4.09	5.62	7.78	4.06	3.84	3.22	2.93	6.28	4.23	3.82
−15	2.56	2.21	4.17	5.12	2.48	3.09	2.67	2.56	4.62	3.97	2.83
−30	2.18	1.19	3.42	2.91	1.50	2.09	1.92	2.10	3.72	0.86	1.60
−60	0.85	0.53	1.47	0.80	0.76	1.01	0.86	0.56	1.96	0.37	0.81
−100	0.41	0.39	0.76	0.27	0.45	0.67	0.36	0.39	0.59	0.17	0.54
Total $CaCO_3$ ($g\,kg^{-1}$)											
−5	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
−15	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
−30	< 1	< 1	< 1	< 1	< 1	< 1	17.00	< 1	19.00	< 1	< 1
−60	< 1	< 1	13.00	2.00	< 1	< 1	33.00	< 1	72.00	7.00	< 1
−100	< 1	13.00	114.00	49.00	< 1	< 1	20.00	< 1	114.00	15.00	2.00

*: mean of 3 replicates

Table D.4: Continued.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
Al oxides (mmol kg^{-1})											
Litter	34.10	21.87	14.82	27.80	24.83	18.16	26.68	40.77	63.38	49.29	35.58
−5	63.38	60.78	48.92	101.55	77.09	86.73	58.56	74.50	55.96	101.18	90.43
−15	64.86	64.49	55.22	126.01	88.95	95.25	59.30	73.01	60.78	104.89	91.17
−30	63.01	58.93	53.00	141.21	95.62	100.07	57.82	70.05	64.12	122.31	95.99
−60	75.24	83.02	61.15	114.52	102.66	116.75	61.89	87.10	62.26	88.95	118.97
−100	64.49	74.12	57.45	81.91	118.23	125.27	53.74	75.61	71.53	92.29	117.12
Fe oxides (mmol kg^{-1})											
Litter	15.40	14.33	6.63	15.76	19.88	12.00	10.92	20.23	23.99	22.20	22.92
−5	31.34	50.68	19.52	56.05	68.05	75.21	25.25	47.81	21.85	48.53	93.65
−15	33.31	53.18	20.41	67.15	75.57	78.97	26.32	47.27	22.20	49.60	95.62
−30	34.20	40.47	19.52	71.45	82.19	89.18	25.43	44.59	22.56	63.75	107.44
−60	35.81	38.50	17.73	65.00	76.28	74.67	24.53	30.08	20.77	55.51	70.19
−100	26.50	33.13	18.26	46.20	67.15	58.55	22.74	30.62	26.86	64.64	59.27
Fine root length density* (cm cm^{-3})											
−5	1.440	2.023	1.995	2.165	0.922	0.772	2.345	4.212	4.025	2.823	2.792
−15	0.773	0.841	1.119	0.944	0.369	0.820	1.301	1.943	1.830	1.025	1.056
−30	0.689	0.395	0.615	0.477	0.163	0.219	0.831	1.167	1.611	0.670	0.294
−60	0.412	0.176	0.259	0.405	0.004	0.011	0.437	0.551	0.628	0.277	0.070
−100	0.328	0.070	0.222	0.083	0.000	0.023	0.112	0.258	0.344	0.018	0.048
Fine root mass density* (mg cm^{-3})											
−5	1.466	1.275	1.347	1.884	0.865	0.873	1.494	1.545	2.303	2.041	1.061
−15	0.565	0.531	0.510	0.870	0.517	0.577	0.593	0.547	0.942	0.488	0.217
−30	0.540	0.221	0.424	0.465	0.226	0.207	0.345	0.309	0.656	0.354	0.051
−60	0.331	0.196	0.133	0.295	0.002	0.007	0.188	0.158	0.298	0.151	0.014
−100	0.412	0.033	0.151	0.072	0.000	0.014	0.060	0.075	0.128	0.004	0.016

*: mean of 3 replicates

Table D.5: Parameters m and n from the model of $r(t)/R$ (Eq. 6.4). "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands) that is to say mainly OL and OF horizons, and eventually OH (at BAR, CHE, KRA and SAE) at the date of sampling.

Depth	Forest						Grassland				
(cm)	BAR	CHE	KRA	SAE	SAW	TOM	BAR	CHE	KRA	SAE	TOM
Parameter m											
Litter	0.924	0.962	0.955	0.953	0.975	0.978	0.984	0.958	0.949	0.969	1.005
−5	0.726	1.024	0.793	0.901	0.953	0.878	0.635	0.646	0.861	0.428	0.745
−15	0.651	0.707	0.556	0.855	0.926	0.634	0.241	0.480	0.401	0.398	0.510
−30	0.526	0.472	0.420	0.235	0.522	0.342	0.161	0.454	0.319	0.087	0.198
−60	0.212	0.087	0.113	0.128	0.153	0.094	0.072	0.072	0.287	0.223	0.036
−100	0.114	0.038	0.077	0.295	0.085	0.028	0.086	0.056	0.101	0.371	0.034
Parameter n											
Litter	0.023	0.028	0.019	0.027	0.024	0.010	0.015	0.000	0.026	0.033	0.003
−5	0.181	0.212	0.163	0.155	0.173	0.385	0.183	0.225	0.157	0.226	0.284
−15	0.214	0.291	0.267	0.213	0.329	0.326	0.230	0.254	0.316	0.313	0.372
−30	0.217	0.313	0.386	0.318	0.370	0.408	0.270	0.288	0.277	0.282	0.427
−60	0.288	0.334	0.262	0.397	0.384	0.392	0.289	0.349	0.299	0.201	0.355
−100	0.337	0.304	0.331	0.290	0.371	0.240	0.280	0.313	0.351	0.307	0.294

Table D.6: Spearman's rank correlation coefficient matrix between P variables and selected soil properties as well as fine root (diameter < 0.8 mm) densities, computed separately for each soil depth investigated. Bold coefficients are significant at $p < 0.05$. Depth is in cm. *Qw*: phosphate ions in solution; *m* and *n* are the fitting parameters of Eq. 6.4; *Pr*: diffusive phosphate ions; *E*: isotopically exchangeable phosphate ions; FRLD: fine root length density; FRMD: fine root mass density.

Variable	P_{tot}	P_{org}	P_{inorg}	*Qw*	*m*	*n*	*Pr* (1 day)	*E* (1 day)
−5 cm depth								
pH	0.100	0.191	-0.109	0.382	-0.300	**-0.700**	0.182	0.182
Clay fraction	0.282	0.500	-0.209	0.300	-0.227	-0.600	0.209	0.245
Organic C	0.300	**0.682**	-0.200	**0.791**	0.500	**-0.773**	**0.655**	**0.673**
$CaCO_3$	na	na	na	na	na	na	na	na
Al oxides	0.355	0.336	-0.091	-0.191	0.000	0.336	-0.191	-0.164
Fe oxides	0.036	0.045	-0.073	-0.209	0.373	0.509	-0.109	-0.109
Al + Fe oxides	0.064	0.173	-0.191	-0.364	0.118	0.555	-0.309	-0.291
P_{tot}	—	0.345	**0.627**	0.527	0.055	-0.409	0.464	0.527
P_{org}	0.345	—	-0.364	0.318	0.227	-0.345	0.100	0.173
P_{inorg}	**0.627**	-0.364	—	0.191	-0.055	0.009	0.364	0.336
Qw	0.527	0.318	0.191	—	**0.609**	**-0.864**	**0.882**	**0.909**
m	0.055	0.227	-0.055	**0.609**	—	-0.318	**0.709**	**0.709**
n	-0.409	-0.345	0.009	**-0.864**	-0.318	—	**-0.673**	**-0.736**
Pr (1 day)	0.464	0.100	0.364	**0.882**	**0.709**	**-0.673**	—	**0.982**
E (1 day)	0.527	0.173	0.336	**0.909**	**0.709**	**-0.736**	**0.982**	—
FRLD	-0.055	0.345	-0.364	-0.145	-0.518	0.018	-0.445	-0.418
FRMD	0.236	0.482	-0.209	0.118	-0.464	-0.364	-0.055	-0.027
−15 cm depth								
pH	0.205	0.318	-0.045	-0.473	**-0.755**	-0.318	-0.227	-0.282
Clay fraction	0.296	**0.609**	-0.291	-0.055	-0.373	-0.491	0.009	0.018
Organic C	0.542	**0.773**	-0.100	0.109	-0.218	-0.536	0.045	0.064
$CaCO_3$	na	na	na	na	na	na	na	na
Al oxides	0.333	0.527	0.036	0.136	0.282	0.155	0.209	0.282
Fe oxides	-0.091	0.027	0.027	0.091	0.455	0.500	0.173	0.227
Al + Fe oxides	0.150	0.336	0.009	0.155	0.409	0.245	0.145	0.227
P_{tot}	—	0.456	**0.688**	0.337	0.018	-0.579	0.296	0.333
P_{org}	0.456	—	-0.091	-0.027	-0.164	-0.118	0.045	0.073
P_{inorg}	**0.688**	-0.091	—	0.209	0.027	-0.309	0.255	0.273
Qw	0.337	-0.027	0.209	—	**0.855**	-0.436	0.600	**0.664**
m	0.018	-0.164	0.027	**0.855**	—	-0.009	0.545	**0.609**
n	-0.579	-0.118	-0.309	-0.436	-0.009	—	0.064	0.000
Pr (1 day)	0.296	0.045	0.255	0.600	0.545	0.064	—	**0.991**
E (1 day)	0.333	0.073	0.273	**0.664**	**0.609**	0.000	**0.991**	—
FRLD	-0.091	0.264	-0.336	**-0.636**	**-0.764**	-0.145	**-0.691**	**-0.736**
FRMD	0.351	0.282	0.064	0.364	-0.018	-0.464	0.400	0.391

Table D.6: Continued.

Variable	P_{tot}	P_{org}	P_{inorg}	Qw	m	n	Pr (1 day)	E (1 day)
–30 cm depth								
pH	0.237	0.273	0.032	0.228	-0.346	**-0.793**	0.533	0.551
Clay fraction	-0.246	0.136	-0.464	-0.036	-0.300	-0.391	0.355	0.282
Organic C	0.400	**0.843**	0.009	0.474	0.328	-0.469	0.077	0.105
$CaCO_3$	0.176	0.324	-0.040	0.027	-0.351	-0.512	0.081	0.081
Al oxides	-0.410	-0.564	-0.209	-0.400	-0.355	0.318	-0.200	-0.291
Fe oxides	-0.305	-0.536	0.018	-0.445	-0.127	0.600	-0.464	-0.536
Al + Fe oxides	-0.465	**-0.636**	-0.209	-0.491	-0.245	0.500	-0.400	-0.491
P_{tot}	—	**0.656**	**0.870**	**0.825**	0.565	**-0.661**	0.205	0.328
P_{org}	**0.656**	—	0.282	**0.691**	0.573	-0.336	0.009	0.100
P_{inorg}	**0.870**	0.282	—	0.573	0.391	-0.500	0.236	0.318
Qw	**0.825**	**0.691**	0.573	—	**0.745**	-0.545	0.445	0.555
m	0.565	0.573	0.391	**0.745**	—	-0.036	0.018	0.109
n	**-0.661**	-0.336	-0.500	-0.545	-0.036	—	-0.473	-0.536
Pr (1 day)	0.205	0.009	0.236	0.445	0.018	-0.473	—	**0.982**
E (1 day)	0.328	0.100	0.318	0.555	0.109	-0.536	**0.982**	—
FRLD	0.387	0.518	0.073	0.336	-0.173	**-0.773**	0.236	0.291
FRMD	0.155	0.336	-0.118	0.427	0.018	**-0.655**	**0.636**	**0.618**
–60 cm depth								
pH	-0.045	0.073	-0.200	0.436	0.400	**-0.636**	-0.491	-0.491
Clay fraction	-0.145	-0.055	-0.082	0.045	-0.555	0.055	**0.782**	**0.782**
Organic C	0.027	0.509	-0.073	0.273	0.209	-0.264	0.182	0.182
$CaCO_3$	-0.312	0.069	-0.461	0.144	0.327	-0.471	**-0.649**	**-0.649**
Al oxides	-0.264	-0.300	-0.127	-0.491	-0.191	**0.718**	0.100	0.100
Fe oxides	-0.164	-0.127	-0.027	-0.482	-0.073	**0.664**	-0.018	-0.018
Al + Fe oxides	-0.264	-0.245	-0.109	-0.564	-0.227	**0.718**	0.027	0.027
P_{tot}	—	0.382	**0.973**	0.555	0.036	-0.427	0.291	0.291
P_{org}	0.382	—	0.282	0.518	0.564	-0.327	-0.091	-0.091
P_{inorg}	**0.973**	0.282	—	0.455	-0.109	-0.355	0.373	0.373
Qw	0.555	0.518	0.455	—	0.509	**-0.809**	0.173	0.173
m	0.036	0.564	-0.109	0.509	—	-0.291	-0.509	-0.509
n	-0.427	-0.327	-0.355	**-0.809**	-0.291	—	0.100	0.100
Pr (1 day)	0.291	-0.091	0.373	0.173	-0.509	0.100	—	**1.000**
E (1 day)	0.291	-0.091	0.373	0.173	-0.509	0.100	**1.000**	—
FRLD	0.318	0.100	0.164	0.327	0.191	-0.373	-0.145	-0.145
FRMD	0.336	0.282	0.200	0.382	0.318	-0.273	-0.100	-0.100

Table D.6: Continued.

Variable	P_{tot}	P_{org}	P_{inorg}	Qw	m	n	Pr (1 day)	E (1 day)
−100 cm depth								
pH	**-0.615**	-0.518	-0.591	-0.364	0.400	-0.109	-0.391	-0.391
Clay fraction	0.308	0.515	0.251	0.451	**-0.847**	-0.105	**0.852**	**0.852**
Organic C	-0.228	0.378	-0.237	**0.679**	-0.287	0.164	0.342	0.342
$CaCO_3$	**-0.673**	-0.359	**-0.676**	-0.284	0.387	-0.019	-0.387	-0.387
Al oxides	0.041	0.073	0.009	0.018	-0.309	-0.164	0.427	0.427
Fe oxides	0.164	-0.118	0.127	-0.127	-0.073	-0.055	0.291	0.291
Al + Fe oxides	0.118	-0.009	0.073	0.000	-0.255	-0.145	0.436	0.436
P_{tot}	—	0.260	**0.989**	0.132	-0.191	0.246	0.241	0.241
P_{org}	0.260	—	0.209	0.409	**-0.709**	0.227	0.500	0.500
P_{inorg}	**0.989**	0.209	—	0.091	-0.145	0.245	0.173	0.173
Qw	0.132	0.409	0.091	—	-0.227	0.555	**0.736**	**0.736**
m	-0.191	**-0.709**	-0.145	-0.227	—	0.300	**-0.655**	**-0.655**
n	0.246	0.227	0.245	0.555	0.300	—	0.291	0.291
Pr (1 day)	0.241	0.500	0.173	**0.736**	**-0.655**	0.291	—	**1.000**
E (1 day)	0.241	0.500	0.173	**0.736**	**-0.655**	0.291	**1.000**	—
FRLD	-0.114	-0.009	-0.055	0.173	0.191	0.273	-0.209	-0.209
FRMD	-0.210	0.073	-0.136	0.100	0.209	0.264	-0.318	-0.318

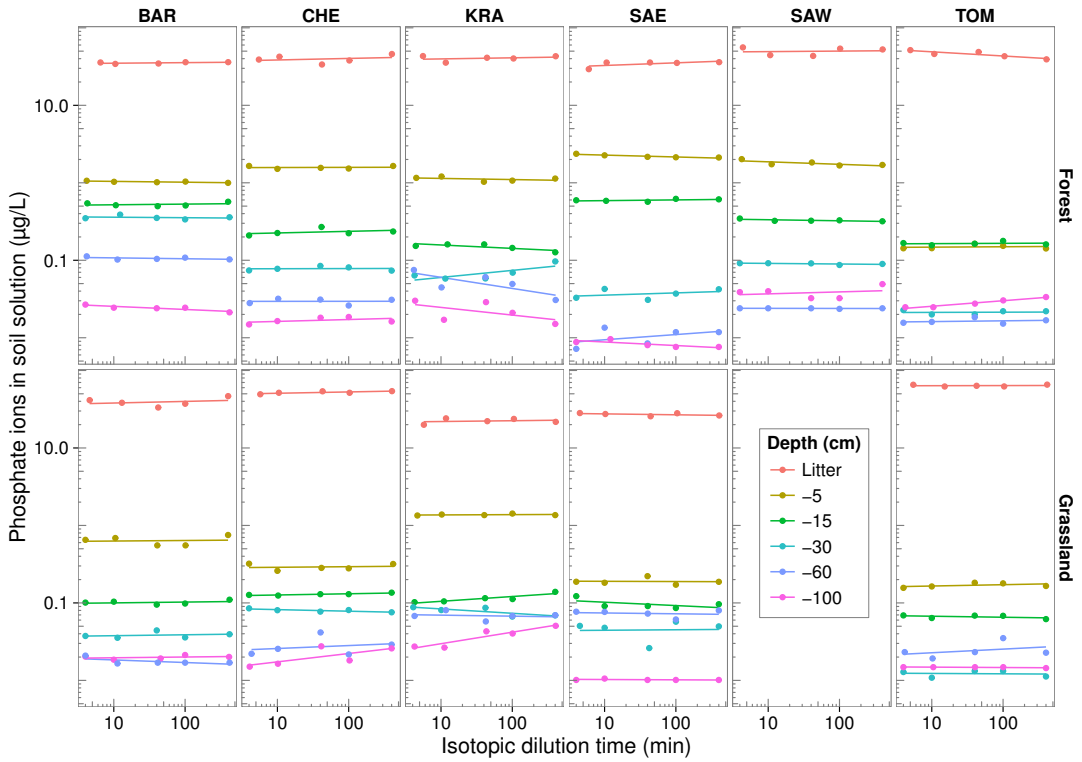


Figure D.1: Measurements of the concentration of phosphate ions in soil solution during the isotopic dilution. "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands) that is to say mainly OL and OF horizons, and eventually OH (at BAR, CHE, KRA and SAE) at the date of sampling.

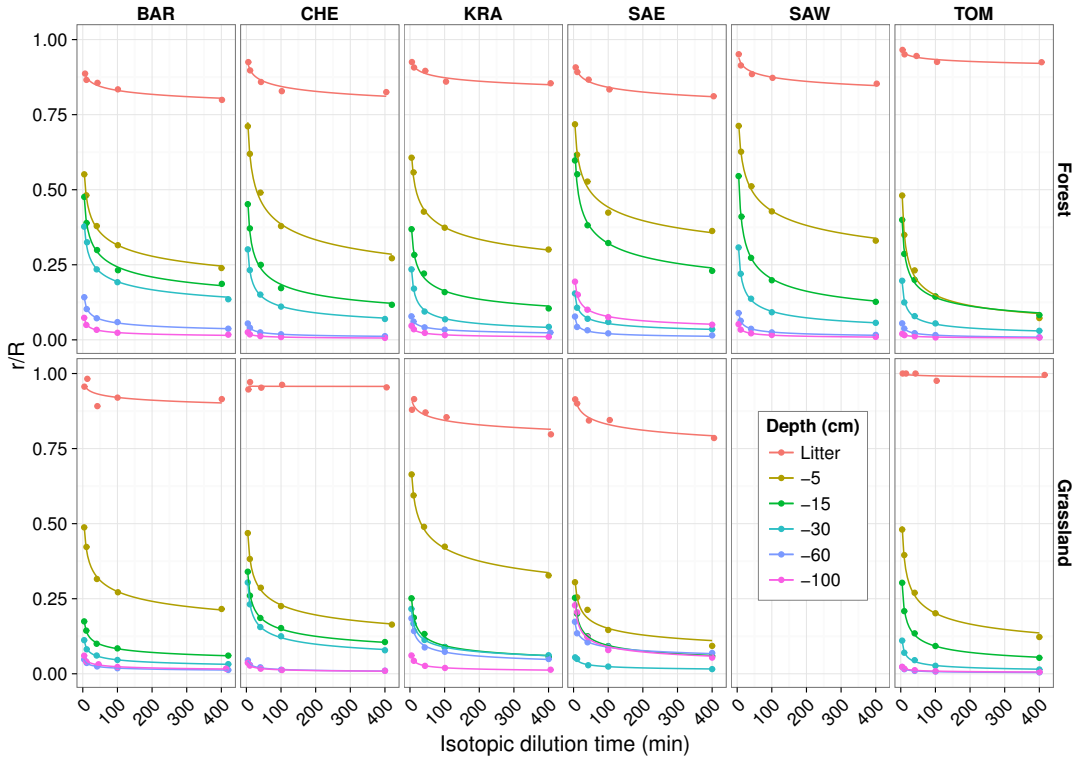


Figure D.2: Fit of the model of $r(t)/R$ (Eq. 6.4). "Litter" means all the dead plant material deposited on the soil surface (senescing leaf litterfall, small branches and senescing understorey vegetation in forests; senescing herbaceous vegetation in grasslands) that is to say mainly OL and OF horizons, and eventually OH (at BAR, CHE, KRA and SAE) at the date of sampling.

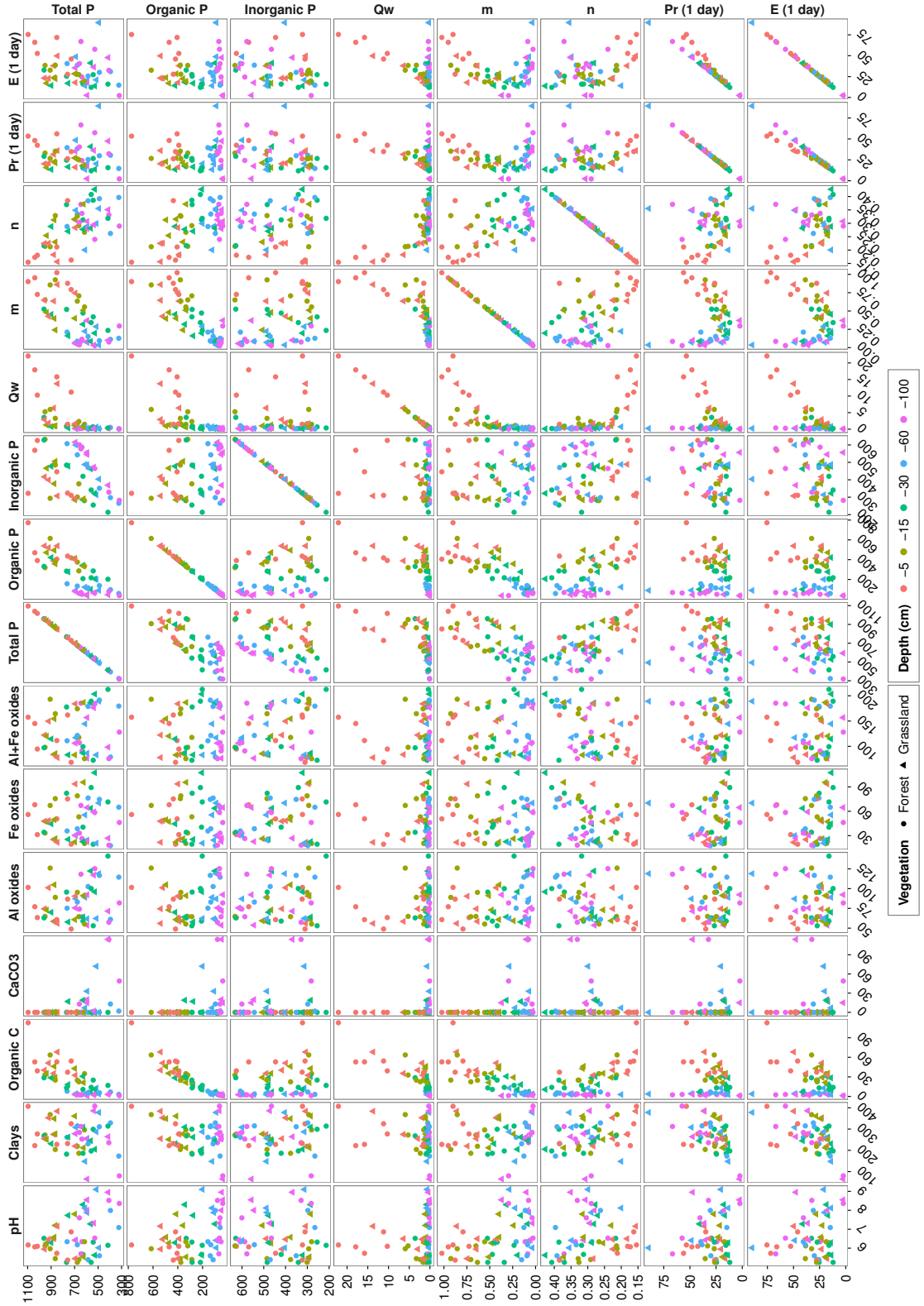


Figure D.3: Matrix of scatter plots of P parameters against soil physico-chemical properties, other P parameters and fine root densities. *Qw*: phosphate ions in solution; *m* and *n* are the fitting parameters of Eq. 6.4; *Pr*: diffusive phosphate ions; *E*: isotopically exchangeable phosphate ions; FRLD: fine root length density; FRMD: fine root mass density.

References of the global data compilation

Abekoe, M. K. and Sahrawat, K. L. (2003). Long-term cropping effect on phosphorus fractions in an ultisol of the humid forest zone in West Africa. *Commun. Soil Sci. Plant Anal.* 34, 427–437.

Achat, D. L., Bakker, M. R., Augusto, L., Derrien, D., Gallegos, N., Lashchinskiy, N., Milin, S., Nikitich, P., Raudina, T., Rusalimova, O., Zeller, B., and Barsukov, P. (2013). Phosphorus status of soils from contrasting forested ecosystems in southwestern Siberia: effects of microbiological and physicochemical properties. *Biogeosciences* 10, 733–752. DOI: 10.5194/bg-10-733-2013.

Achat, D. L., Pousse, N., Nicolas, M., Brédoire, F., and Augusto, L. (2016). Soil properties controlling inorganic phosphorus availability – Generic results from a national forest network and a global compilation of the literature. *Biogeochemistry*.

Achat, D. L., Augusto, L., Morel, C., and Bakker, M. R. (2011). Predicting available phosphate ions from physical–chemical soil properties in acidic sandy soils under pine forests. *J. Soils Sediments* 11 (3), 452–466. DOI: 10.1007/s11368-010-0329-9.

Achat, D. L., Bakker, M. R., Augusto, L., Saur, E., Dousseron, L., and Morel, C. (2009). Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods. *Biogeochemistry* 92 (3), 183–200. DOI: 10.1007/s10533-008-9283-7.

Achat, D. L., Daumer, M.-L., Sperandio, M., Santellani, A.-C., and Morel, C. (2014). Solubility and mobility of phosphorus recycled from dairy effluents and pig manures in incubated soils with different characteristics. *Nutri. Cycl. Agroecosyst.* 99.1-3, 1–15. DOI: 10.1007/s10705-014-9614-0.

Agbenin, J. O. and Goladi, J. T. (1998). Dynamics of phosphorus fractions in a savanna Alfisol under continuous cultivation. *Soil Use and Management* 14, 59–64.

Agbenin, J. O. and Igbokwe, S. O. (2006). Effect of soil-dung manure incubation on the solubility and retention of applied phosphate by a weathered tropical semi-arid soil. *Geoderma* 133, 191–203. DOI: 10.1016/j.geoderma.2005.07.006.

Agbenin, J. O. and Tiessen, H. (1994). Phosphorus Transformations in a Toposequence of Lithosols and Cambisols from Semiarid Northeastern Brazil. *Geoderma* 62, 345–362. DOI: 10.1016/0016-7061(94)90098-1.

Aguiar, A. D. F., Candido, C. S., Carvalho, C. S., Monroe, P. H. M., and Moura, E. G. de (2013). Organic matter fraction and pools of phosphorus as indicators of the impact of land use in the Amazonian periphery. *Ecol. Indic.* 30, 158–164. DOI: 10.1016/j.ecolind.2013.02.010.

Almond, P. C. and Tonkin, P. J. (1999). Pedogenesis by upbuilding in an extreme leaching and weathering environment, and slow loess accretion, south Westland, New Zealand. *Geoderma* 92, 1–36. DOI: 10.1016/S0016-7061(99)00016-6.

Alt, F., Oelmann, Y., Herold, N., Schrumpf, M., and Wilcke, W. (2011). Phosphorus partitioning in grassland and forest soils of Germany as related to land-use type, management intensity, and land use-related pH. *J. Plant Nutr. Soil Sci.* 174, 195–209. DOI: 10.1002/jpln.201000142.

Andersohn, C. (1996). Phosphate cycles in energy crop systems with emphasis on the availability of different phosphate fractions in the soil. *Plant Soil* 184, 11–21. DOI: 10.1007/Bf00029270.

Andriamaniraka, H., Rabeharisoa, L., Michellon, R., Moussa, N., and Morel, C. (2010). Influence de différents systèmes de culture sur la productivité de sols cultivés des Hautes Terres de Madagascar et conséquences pour le bilan de phosphore. *Étude et Gestion des Sols* 17.2, 119–130.

Aoki, M., Fujii, K., and Kitayama, K. (2012). Environmental Control of Root Exudation of Low-Molecular Weight Organic Acids in Tropical Rainforests. *Ecosystems* 15, 1194–1203. DOI: 10.1007/s10021-012-9575-6.

Aulakh, M. S., Kabba, B. S., Baddesha, H. S., Bahl, G. S., and Gill, M. P. S. (2003). Crop yields and phosphorus fertilizer transformations after 25 years of applications to a subtropical soil under groundnut-based cropping systems. *Field Crops Research* 83, 283–296.

Bah, A. R., Zaharah, A. R., Hussin, A., Husni, M. H., and Halimi, M. S. (2003). Phosphorus status of amended soil as assessed by conventional and isotopic methods. *Commun. Soil Sci. Plant Anal.* 34.17-18, 2659–2681. DOI: 10.1081/css-120024792.

Basamba, T. A., Barrios, E., Singh, B. R., and Rao, I. M. (2007). Impact of planted fallows and a crop rotation on nitrogen mineralization and phosphorus and organic matter fractions on a Colombian volcanic-ash soil. *Nutri. Cycl. Agroecosyst.* 77, 127–141. DOI: 10.1007/s10705-006-9050-x.

Beck, M. A. and Elsenbeer, H. (1999). Biogeochemical cycles of soil phosphorus in southern Alpine spodosols. *Geoderma* 91, 249–260.

Beck, M. A. and Sanchez, P. A. (1996). Soil phosphorus movement and budget after 13 years of fertilized cultivation in the Amazon basin. *Plant Soil* 184, 23–31.

Blake, L., Johnston, A. E., Poulton, P. R., and Goulding, K. W. T. (2003). Changes in soil phosphorus fractions following positive and negative phosphorus balances for long periods. *Plant Soil* 254, 245–261. DOI: 10.1023/A:1025544817872.

Boldeskul, A. G. (2002). The forms of phosphorus compounds in brown soils of fir-broad-leaved forests of the southern Primor'e Region. *Eurasian Soil Sci.* 35, 71–78.

Borda, T., Celi, L., Bünemann, E. K., Oberson, A., Frossard, E., and Barberis, E. (2014). Fertilization strategies affect phosphorus forms and release from soils and suspended solids. *Journal of Environment Quality* 43.3, 1024. DOI: 10.2134/jeq2013.11.0436.

Brandtberg, P. O., Davis, M. R., Clinton, P. W., Condron, L. M., and Allen, R. B. (2010). Forms of soil phosphorus affected by stand development of mountain beech (*Nothofagus*) forests in New Zealand. *Geoderma* 157, 228–234.

Bühler, S., Oberson, A., Rao, I. M., Friesen, D. K., and Frossard, E. (2002). Sequential phosphorus extraction of a P-labeled oxisol under contrasting agricultural systems. *Soil Sci. Soc. Am. J.* 66.3, 868–877. DOI: 10.2136/sssaj2002.0868.

Bühler, S., Oberson, A., Sinaj, S., Friesen, D. K., and Frossard, E. (2003). Isotope methods for assessing plant available phosphorus in acid tropical soils. *Eur. J. Soil Sci.* 54.3, 605–616. DOI: 10.1046/j.1365-2389.2003.00542.x.

Bünemann, E. K., Marschner, P., McNeill, A., and McLaughlin, M. (2007). Measuring rates of gross and net mineralisation of organic phosphorus in soils. *Soil Biol. Biochem.* 39.4, 900–913. DOI: 10.1016/j.soilbio.2006.10.009.

Bünemann, E. K., Steinebrunner, F., Smithson, P. C., Frossard, E., and Oberson, A. (2004). Phosphorus dynamics in a highly weathered soil as revealed by isotopic labeling techniques. *Soil Sci. Soc. Am. J.* 68.5, 1645–1655. DOI: 10.2136/sssaj2004.1645.

Bünemann, E., Oberson, A., Liebisch, F., Keller, F., Annaheim, K., Huguenin-Elie, O., and Frossard, E. (2012). Rapid microbial phosphorus immobilization dominates gross phosphorus fluxes in a grassland soil with low inorganic phosphorus availability. *Soil Biol. Biochem.* 51, 84–95. DOI: 10.1016/j.soilbio.2012.04.012.

Bünemann, E. K. (2003). Phosphorus dynamics in a ferralsol under maize-fallow rotations: The role of the soil microbial biomass. PhD thesis. ETH, Swiss Federal Institute of Technology.

Campbell, C. A., Schnitzer, M., Stewart, J. W. B., Biederbeck, V. O., and Selles, F. (1986). Effect of manure and P fertilizer on properties of a black chernozem in southern Saskatchewan. *Can. J. Soil Sci.* 66, 601–613.

Cassagne, N., Remaury, M., Gauquelin, T., and Fabre, A. (2000). Forms and profile distribution of soil phosphorus in alpine Inceptisols and Spodosols (Pyrenees, France). *Geoderma* 95, 161–172.

Chacon, N. and Dezzeo, N. (2004). Phosphorus fractions and sorption processes in soil samples taken in a forest-savanna sequence of the Gran Sabana in southern Venezuela. *Biol. Fertil. Soils* 40, 14–19.

Chacon, N., Dezzeo, N., Munoz, B., and Rodriguez, J. M. (2005). Implications of soil organic carbon and the biogeochemistry of iron and aluminum on soil phosphorus distribution in flooded forests of the lower Orinoco River, Venezuela. *Biogeochemistry* 73, 555–566. DOI: 10.1007/s10533-004-1773-7.

Chapuis-Lardy, L., Ramiandrisoa, R. S., Randriamanantsoa, L., Morel, C., Rabeharisoa, L., and Blanchart, E. (2009). Modification of P availability by endogeic earthworms (Glossoscolecidae) in Ferralsols of the Malagasy Highlands. *Biol. Fertil. Soils* 45.4, 415–422. DOI: 10.1007/s00374-008-0350-y.

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L. S., and Meerts, P. (2006). Effect of the exotic invasive plant Solidago gigantea on soil phosphorus status. *Biol. Fertil. Soils* 42, 481–489. DOI: 10.1007/s00374-005-0039-4.

Chen, C. R., Condron, L. M., Davis, M. R., and Sherlock, R. R. (2003a). Seasonal changes in soil phosphorus and associated microbial properties under adjacent grassland and forest in New Zealand. *For. Ecol. Manage.* 177, 539–557.

Chen, C. R., Condron, L. M., Sinaj, S., Davis, M. R., Sherlock, R. R., and Frossard, E. (2003b). Effects of plant species on phosphorus availability in a range of grassland soils. *Plant Soil* 256.1, 115–130. DOI: 10.1023/a:1026273529177.

Chen, C., Sinaj, S., Condron, L., Frossard, E., Sherlock, R., and Davis, M. (2003c). Characterization of phosphorus availability in selected New Zealand grassland soils. *Nutri. Cycl. Agroecosyst.* 65 (1), 89–100. DOI: 10.1023/A:1021889207109.

Chen, F. S., Li Xi, G. N., and Zhan, S. X. (2010). Topsoil phosphorus signature in five forest types along an urban-suburban-rural gradient in Nanchang, southern China. *Journal of Forestry Research* 21, 39–44.

Chimdi, A., Esala, M., and Ylivainio, K. (2014). Sequential Fractionation Patterns of Soil Phosphorus Collected from Different Land Use Systems of Dire Inchine District, West Shawa Zone, Ethiopia. *American-Eurasian Journal of Scientific Research* 9, 51–57.

Chiu, C. Y., Pai, C. W., and Yang, K. L. (2005). Characterization of phosphorus in sub-alpine forest and adjacent grassland soils by chemical extraction and phosphorus-31 nuclear magnetic resonance spectroscopy. *Pedobiologia* 49, 655–663. DOI: 10.1016/j.pedobi.2005.06.007.

Ciampitti, I. A., Picone, L. I., Rubio, G., and Garcia, F. O. (2011). Pathways of Phosphorous Fraction Dynamics in Field Crop Rotations of the Pampas of Argentina. *Soil Sci. Soc. Am. J.* 75, 918–926. DOI: 10.2136/sssaj2010.0361.

Cleveland, C. C., Townsend, A. R., Schmidt, S. K., and Constance, B. C. (2003). Soil microbial dynamics and biogeochemistry in tropical forests and pastures, southwestern Costa Rica. *Ecol. Appl.* 13, 314–326. DOI: 10.1890/1051-0761(2003)013[0314:Smdabi]2.0.Co;2.

Compaoré, E., Frossard, E., Sinaj, S., Fardeau, J.-C., and Morel, J.-L. (2003). Influence of land-use management on isotopically exchangeable phosphate in soils from Burkina Faso. *Commun. Soil Sci. Plant Anal.* 34.1-2, 201–223. DOI: 10.1081/css-120017426.

Compton, J. E. and Cole, D. W. (2001). Fate and effects of phosphorus additions in soils under N-2-fixing red alder. *Biogeochemistry* 53, 225–247. DOI: 10.1023/A:1010646709944.

Condron, L. M., Davis, M. R., Newman, R. H., and Cornforth, I. S. (1996). Influence of conifers on the forms of phosphorus in selected New Zealand grassland soils. *Biol. Fertil. Soils* 21, 37–42. DOI: 10.1007/Bf00335991.

Couto, R. D., Santos, M. dos, Comin, J. J., Martini, L. C. P., Gatiboni, L. C., Martins, S. R., Belli, P., and Brunetto, G. (2015). Environmental Vulnerability and Phosphorus Fractions of Areas with Pig Slurry Applied to the Soil. *J. Environ. Qual.* 44, 162–173. DOI: 10.2134/jeq2014.08.0359.

Crews, T. E. (1996). The supply of phosphorus from native, inorganic phosphorus pools in continuously cultivated Mexican agroecosystems. *Agric. Ecosyst. Environ.* 57, 197–208.

Crews, T. E. and Brookes, P. C. (2014). Changes in soil phosphorus forms through time in perennial versus annual agroecosystems. *Agric. Ecosyst. Environ.* 184, 168–181. DOI: 10.1016/j.agee.2013.11.022.

Cross, A. F. and Schlesinger, W. H. (2001). Biological and geochemical controls on phosphorus fractions in semiarid soils. *Biogeochemistry* 52, 155–172. DOI: 10.1023/A:1006437504494.

De Schrijver, A., Vesterdal, L., Hansen, K., De Frenne, P., Augusto, L., Achat, D. L., Staelens, J., Baeten, L., De Keersmaeker, L., De Neve, S., and Verheyen, K. (2012). Four decades of post-agricultural forest development have caused major redistributions of soil phosphorus fractions. *Oecologia* 169, 221–234. DOI: 10.1007/s00442-011-2185-8.

Delgado, A. and Torrent, J. (1997). Phosphate-rich soils in the European Union: estimating total plant-available phosphorus. *Eur. J. Agron.* 6.3-4, 205–214. DOI: 10.1016/s1161-0301(96)02048-5.

Demaria, P. (2004). Factors controlling phosphate exchangeability and release in agricultural soils. PhD thesis. ETH, Swiss Federal Institute of Technology.

Demaria, P., Sinaj, S., Flisch, R., and Frossard, E. (2013). Soil properties and phosphorus isotopic exchangeability in cropped temperate soils. *Commun. Soil Sci. Plant Anal.* 44.1-4, 287–300. DOI: 10.1080/00103624.2013.741896.

Derry, D. D., Voroney, R. P., and Briceno, J. A. (2005). Long-term effects of short-fallow frijol tapado on soil phosphorus pools in Costa Rica. *Agric. Ecosyst. Environ.* 110, 91–103. DOI: 10.1016/j.agee.2005.05.006.

Diekmann, L. O. (2004). *Soil nutrient dynamics during shifting cultivation in Campeche, Mexico.* Tech. rep., p. 85.

Dieter, D., Elsenbeer, H., and Turner, B. L. (2010). Phosphorus fractionation in lowland tropical rainforest soils in central Panama. *Catena* 82, 118–125. DOI: 10.1016/j.catena.2010.05.010.

Dobermann, A., George, T., and Thevs, N. (2002). Phosphorus fertilizer effects on soil phosphorus pools in acid upland soils. *Soil Sci. Soc. Am. J.* 66, 652–660.

Dodd, R. J. (2013). Use less, lose less: Obtaining and maintaining an environmentally and agronomically sustainable farming system with phosphorus. PhD thesis. Lincoln University.

Dormaar, J. F. and Willms, W. D. (2000). A comparison of soil chemical characteristics in modified rangeland communities. *J. Range Manage.* 53, 453–458. DOI: 10.2307/4003759.

Duffera, M. and Robarge, W. P. (1999). Soil characteristics and management effects on phosphorus sorption by highland plateau soils of Ethiopia. *Soil Sci. Soc. Am. J.* 63, 1455–1462.

Elpat'evskii, P. V. (1998). Stores and dynamics of available phosphorus in brown forest soils of southern primorye forests in the Far East. *Eurasian Soil Sci.* 31, 54–60.

Esberg, C., Toit, B. du, Olsson, R., Ilstedt, U., and Giesler, R. (2010). Microbial responses to P addition in six South African forest soils. *Plant Soil* 329, 209–225. DOI: 10.1007/s11104-009-0146-3.

Fabre, A., Pinay, G., and Ruffinoni, C. (1996). Seasonal changes in inorganic and organic phosphorus in the soil of a riparian forest. *Biogeochemistry* 35, 419–432. DOI: 10.1007/Bf02183034.

Fan, J., Wang, J. Y., Hu, X. F., and Chen, F. S. (2014). Seasonal dynamics of soil nitrogen availability and phosphorus fractions under urban forest remnants of different vegetation communities in Southern China. *Urban For. Urban Greening* 13, 576–585. DOI: 10.1016/j.ufug.2014.03.002.

Fardeau, J. C., Morel, C., and Jappe, J. (1985). Cinétique d'échange des ions phosphate dans les systèmes sol-solution. Vérification expérimentale de l'équation théorique. In: *C.R. Acad. Sci. Paris, t 300, série III 8*, 371–376.

Fardeau, J. (1993). Le phosphore biodisponible du sol. Un système pluricompartimental à structure mamellaire. *Agronomie* 1, 1–13.

Fardeau, J., Morel, C., and Boniface, R. (1991). Cinétiques de transfert des ions phosphate du sol vers la solution du sol : paramètres caractéristiques. *Agronomie* 11.9, 787–797. DOI: 10.1051/agro:19910909.

Finzi, A. C. (2009). Decades of atmospheric deposition have not resulted in widespread phosphorus limitation or saturation of tree demand for nitrogen in southern New England. *Biogeochemistry* 92, 217–229. DOI: 10.1007/s10533-009-9286-z.

Frizano, J., Johnson, A. H., Vann, D. R., and Scatena, F. N. (2002). Soil phosphorus fractionation during forest development on landslide scars in the Luquillo Mountains, Puerto Rico. *Biotropica* 34, 17–26.

Frizano, J., Vann, D. R., Johnson, A. H., Johnson, C. M., Vieira, I. C. G., and Zarin, D. J. (2003). Labile phosphorus in soils of forest fallows and primary forest in the Bragantina region, Brazil. *Biotropica* 35, 2–11.

Frossard, E., Bolomey, S., Flura, T., and Sinaj, S. (2005). Phosphore du sol et stratégie de fertilisation. Le cas du lac de Baldegg. In: *Documents environnement*. Vol. 206.

Frossard, E., López-Hernández, D., and Brossard, M. (1996). Can isotopic exchange kinetics give valuable information on the rate of mineralization of organic phosphorus in soils? *Soil Biol. Biochem.* 28.7, 857–864. DOI: 10.1016/0038-0717(96)00063-6.

Frossard, E., Morel, J. L., Fardeau, J. C., and Brossard, M. (1994). Soil isotopically exchangeable phosphorus: A comparison between E and L values. *Soil Sci. Soc. Am. J.* 58.3, 846–851. DOI: 10.2136/sssaj1994.03615995005800030031x.

Frossard, E., Stewart, J. W. B., and St-Arnaud, R. J. (1989). Distribution and mobility of phosphorus in grassland and forest soils of Saskatchewan. *Can. J. Soil Sci.* 69.2, 401–416. DOI: 10.4141/cjss89-040.

Frossard, E., Achat, D., Bernasconi, S., Bünemann, E., Fardeau, J.-C., Jansa, J., Morel, C., Rabeharisoa, L., Randriamanantsoa, L., Sinaj, S., Tamburini, F., and Oberson, A. (2011). The use of tracers to investigate phosphate cycling in soil–-plant systems. In: *Phosphorus in Action*. Vol. 100, 59–91. DOI: 10.1007/978-3-642-15271-9_3.

Gabbasova, I. M., Sirayeva, E. Z., Kol'tsova, G. A., and Khakimova, G. A. (1993). Content and composition of organic phosphates in the soils of Bashkiria. *Eurasian Soil Sci.* 25, 36–48.

Galang, M. A., Markewitz, D., and Morris, L. A. (2010). Soil phosphorus transformations under forest burning and laboratory heat treatments. *Geoderma* 155, 401–408. DOI: 10.1016/j.geoderma.2009.12.026.

Gallet, A., Flisch, R., Ryser, J.-P., Frossard, E., and Sinaj, S. (2003). Effect of phosphate fertilization on crop yield and soil phosphorus status. *J. Plant Nutr. Soil Sci.* 166.5, 568–578. DOI: 10.1002/jpln.200321081.

Garcia-Montiel, D. C., Neill, C., Melillo, J., Thomas, S., Steudler, P. A., and Cerri, C. C. (2000). Soil phosphorus transformations following forest clearing for pasture in the Brazilian Amazon. *Soil Sci. Soc. Am. J.* 64, 1792–1804.

Gazizullin, A. K. and Sabirov, A. T. (1991). Iron oxides in major types of Forest soils of the Middle Volga Region. *Soviet Soil Science* 23, 84–102.

Giardina, C. P., Sanford, R. L., and Dockersmith, I. C. (2000). Changes in soil phosphorus and nitrogen during slash-and-burn clearing of a dry tropical forest. *Soil Sci. Soc. Am. J.* 64, 399–405.

Gichangi, E. M., Mnkeni, P. N. S., and Brookes, P. C. (2009). Effects of goat manure and inorganic phosphate addition on soil inorganic and microbial biomass phosphorus fractions under laboratory incubation conditions. *Soil Sci. Plant Nutr.* 55, 764–771. DOI: 10.1111/j.1747-0765.2009.00415.x.

Gleason, S. M., Read, J., Ares, A., and Metcalfe, D. J. (2009). Phosphorus economics of tropical rainforest species and stands across soil contrasts in Queensland, Australia: understanding the effects of soil specialization and trait plasticity. *Funct. Ecol.* 23, 1157–1166. DOI: 10.1111/j.1365-2435.2009.01575.x.

Gorbachev, V. N. and Popova, E. P. (1984). Characteristics of soil formation on loesslike loams in the southern taiga of central Siberia. *Soviet Soil Science* 16, 12–18.

Gressel, N., Mccoll, J. G., Preston, C. M., Newman, R. H., and Powers, R. F. (1996). Linkages between phosphorus transformations and carbon decomposition in a forest soil. *Biogeochemistry* 33, 97–123. DOI: 10.1007/Bf02181034.

Guardini, R., Comin, J. J., Schmitt, D. E., Tiecher, T., Bender, M. A., Santos, D. R. dos, Mezzari, C. P., Oliveira, B. S., Gatiboni, L. C., and Brunetto, G. (2012). Accumulation of phosphorus fractions in typic Hapludalf soil after long-term application of pig slurry and deep pig litter in a no-tillage system. *Nutri. Cycl. Agroecosyst.* 93, 215–225. DOI: 10.1007/s10705-012-9511-3.

Gundale, M. J., Sutherland, S., and DeLuca, T. H. (2008). Fire, native species, and soil resource interactions influence the spatio-temporal invasion pattern of Bromus tectorum. *Ecography* 31, 201–210. DOI: 10.1111/j.0906-7590.2008.5303.x.

Haefele, S. M., Wopereis, M. C. S., Schloebohm, A. M., and Wiechmann, H. (2004). Long-term fertility experiments for irrigated rice in the West African Sahel: effect on soil characteristics. *Field Crops Research* 85, 61–77. DOI: 10.1016/S0378-4290(03)00153-9.

Hamon, R. E. and McLaughlin, M. J. (2002). Interferences in the determination of isotopically exchangeable P in soils and a method to minimise them. *Aust. J. Soil Res.* 40.8, 1383–1397. DOI: 10.1071/sr02045.

Hartono, A., Funakawa, S., and Kosaki, T. (2006). Transformation of added phosphorus to acid upland soils with different soil properties in Indonesia. *Soil Sci. Plant Nutr.* 52, 734–744. DOI: 10.1111/j.1747-0765.2006.00087.x.

Hashimoto, Y. and Watanabe, Y. (2014). Combined applications of chemical fractionation, solution P-31-NMR and P K-edge XANES to determine phosphorus speciation in soils formed on serpentine landscapes. *Geoderma* 230, 143–150. DOI: 10.1016/j.geoderma.2014.04.001.

Heinrich, P. A. and Patrick, J. W. (1985). Phosphorus Acquisition in the Soil Root-System of Eucalyptus-Pilularis Sm Seedlings .1. Characteristics of the Soil System. *Aust. J. Soil Res.* 23, 223–236. DOI: 10.1071/Sr9850223.

Hernández, G., Cuenca, G., and García, A. (2000). Behaviour of arbuscular-mycorrhizal fungi on Vigna luteola growth and its effect on the exchangeable (32 P) phosphorus of soil. *Biol. Fertil. Soils* 31.3-4, 232–236. DOI: 10.1007/s003740050650.

Hu, X. F., Chen, F. S., Nagle, G., Fang, Y. T., and Yu, M. Q. (2011). Soil phosphorus fractions and tree phosphorus resorption in pine forests along an urban-to-rural gradient in Nanchang, China. *Plant Soil* 346, 97–106. DOI: 10.1007/s11104-011-0799-6.

Ilstedt, U., Giesler, R., Nordgren, A., and Malmer, A. (2003). Changes in soil chemical and microbial properties after a wildfire in a tropical rainforest in Sabah, Malaysia. *Soil Biol. Biochem.* 35, 1071–1078. DOI: 10.1016/S0038-0717(03)00152-4.

Imai, N., Kitayama, K., and Titin, J. (2010). Distribution of phosphorus in an above-to-below-ground profile in a Bornean tropical rain forest. *J. Trop. Ecol.* 26, 627–636. DOI: 10.1017/S0266467410000350.

Izquierdo, J. E., Houlton, B. Z., and Huysen, T. L. van (2013). Evidence for progressive phosphorus limitation over long-term ecosystem development: Examination of a biogeochemical paradigm. *Plant Soil* 367, 135–147. DOI: 10.1007/s11104-013-1683-3.

Keller, M., Oberson, A., Annaheim, K. E., Tamburini, F., Mader, P., Mayer, J., Frossard, E., and Bunemann, E. K. (2012). Phosphorus forms and enzymatic hydrolyzability of organic phosphorus in soils after 30 years of organic and conventional farming. *J. Plant Nutr. Soil Sci.* 175, 385–393. DOI: 10.1002/jpln.201100177.

Khan, K. S. and Joergensen, R. G. (2012). Relationships between P fractions and the microbial biomass in soils under different land use management. *Geoderma* 173, 274–281. DOI: 10.1016/j.geoderma.2011.12.022.

Kitayama, K., Aiba, S. I., Takyu, M., Majalap, N., and Wagai, R. (2004). Soil phosphorus fractionation and phosphorus-use efficiency of a Bornean tropical montane rain forest during soil aging with podozolization. *Ecosystems* 7, 259–274. DOI: 10.1007/s10021-003-0229-6.

Kolahchi, Z. and Jalali, M. (2012). Speciation of Phosphorus in Phosphorus-Amended and Leached Calcareous Soils Using Chemical Fractionation. *Pol. J. Environ. Stud.* 21, 395–400.

Kolawole, G. O., Tijani-Eniola, H., and Tian, G. (2004). Phosphorus fractions in fallow systems of West Africa: Effect of residue management. *Plant Soil* 263, 113–120. DOI: 10.1023/B:Plso.0000047730.58844.B5.

Kristiansen, S. M., Amelung, W., and Zech, W. (2001). Phosphorus forms as affected by abandoned anthills (Formica polyctena Forster) in forest soils: sequential extraction and liquid-state P-31-NMR spectroscopy. *J. Plant Nutr. Soil Sci.* 164, 49–55. DOI: 10.1002/1522-2624(200102)164:1<49::Aid-Jpln49>3.0.Co;2-X.

Krivonosova, G. M. and Basevich, T. V. (1980). Content and forms of organic phosphates in the soils of the steppe zone of the Ukraine [USSR]. *Soviet Soil Science* 12, 290–294.

Kuczak, C. N., Fernandes, E. C. M., Lehmann, J., Rondon, M. A., and Luizao, F. J. (2006). Inorganic and organic phosphorus pools in earthworm casts (Glossoscolecidae) and a Brazilian rainforest Oxisol. *Soil Biol. Biochem.* 38, 553–560. DOI: 10.1016/j.soilbio.2005.06.007.

Kunito, T., Tsunekawa, M., Yoshida, S., Park, H. D., Toda, H., Nagaoka, K., and Saeki, K. (2012). Soil Properties Affecting Phosphorus Forms and Phosphatase Activities in Japanese Forest Soils: Soil Microorganisms May Be Limited by Phosphorus. *Soil Sci.* 177, 39–46. DOI: 10.1097/SS.0b013e3182378153.

Kvarnstrom, E., Morel, C., Fardeau, J.-C., Morel, J.-L., and Esa, S. (2000). Changes in the phosphorus availability of a chemically precipitated urban sewage sludge as a result of different dewatering processes. *Waste Manage. Res.* 18.3, 249–258. DOI: 10.1177/0734242x0001800306.

Lan, Z. M., Lin, X. J., Wang, F., Zhang, H., and Chen, C. R. (2012). Phosphorus availability and rice grain yield in a paddy soil in response to long-term fertilization. *Biol. Fertil. Soils* 48, 579–588. DOI: 10.1007/s00374-011-0650-5.

Lee, D., Han, X. G., and Jordan, C. F. (1990). Soil-Phosphorus Fractions, Aluminum, and Water-Retention as Affected by Microbial Activity in an Ultisol. *Plant Soil* 121, 125–136. DOI: 10.1007/Bf00013105.

Lehmann, J., Gunther, D., Mota, M. S. da, Almeida, M. P. de, Zech, W., and Kaiser, K. (2001). Inorganic and organic soil phosphorus and sulfur pools in an Amazonian multistrata agroforestry system. *Agrofor. Syst.* 53, 113–124. DOI: 10.1023/A:1013364201542.

Levy, E. T. and Schlesinger, W. H. (1999). A comparison of fractionation methods for forms of phosphorus in soils. *Biogeochemistry* 47, 25–38. DOI: 10.1023/A:1006105420235.

Li, L., Liang, X. Q., Ye, Y. S., Zhao, Y., Zhang, Y. X., Jin, Y., Yuan, J. L., and Chen, Y. X. (2015a). Effects of repeated swine manure applications on legacy phosphorus and phosphomonoesterase activities in a paddy soil. *Biol. Fertil. Soils* 51, 167–181. DOI: 10.1007/s00374-014-0956-1.

Li, Y. F., Luo, A. C., Wei, X. H., and Yao, X. G. (2008). Changes in Phosphorus Fractions, pH, and Phosphatase Activity in Rhizosphere of Two Rice Genotypes. *Pedosphere* 18, 785–794. DOI: 10.1016/S1002-0160(08)60074-0.

Li, Y. Y., Yang, R., Gao, R., Wei, H. A., Chen, A. L., and Li, Y. (2015b). Effects of long-term phosphorus fertilization and straw incorporation on phosphorus fractions in subtropical paddy soil. *Journal of Integrative Agriculture* 14, 365–373. DOI: 10.1016/S2095-3119(13)60684-X.

Liu, Q., Loganathan, P., Hedley, M. J., and Skinner, M. F. (2004). The mobilisation and fate of soil and rock phosphate in the rhizosphere of ectomycorrhizal Pinus radiata seedlings in an Allophanic soil. *Plant Soil* 264, 219–229. DOI: 10.1023/B:Plso.0000047758.77661.57.

Lopez-Hernandez, D., Brossard, M., and Frossard, E. (1998). P-Isotopic exchange values in relation to Po mineralisation in soils with very low P-sorbing capacities. *Soil Biol. Biochem.* 30.13, 1663–1670. DOI: 10.1016/s0038-0717(97)00255-1.

Magid, J. (1993). Vegetation Effects on Phosphorus Fractions in Set-Aside Soils. *Plant Soil* 149, 111–119. DOI: 10.1007/Bf00010768.

Makarov, M. I., Malysheva, T. I., Vladychenskii, A. S., and Zech, W. (2002). Phosphorus compounds in primitive soils on mantle loam under various phytocenoses. *Eurasian Soil Sci.* 35, 924–933.

Makarov, M. I., Volkov, A. V., Malysheva, T. I., and Onipchenko, V. G. (2001). Phosphorus, nitrogen, and carbon in the soils of subalpine and alpine altitudinal belts of the Teberda Nature Reserve. *Eurasian Soil Sci.* 34, 52–60.

Malik, M. A., Khan, K. S., Fayyaz-ul-Hassan, and Umair, A. (2014). Dynamics of Phosphorus Pools in Subtropical Alkaline Soils. *International Journal of Agriculture and Biology* 16, 293–299.

Markewitz, D., Figueiredo, R. D., Carvalho, C. J. R. de, and Davidson, E. A. (2012). Soil and tree response to P fertilization in a secondary tropical forest supported by an Oxisol. *Biol. Fertil. Soils* 48, 665–678. DOI: 10.1007/s00374-011-0659-9.

McGrath, D. A., Duryea, M. L., and Cropper, W. P. (2001). Soil phosphorus availability and fine root proliferation in Amazonian agroforests 6 years following forest conversion. *Agric. Ecosyst. Environ.* 83, 271–284. DOI: 10.1016/S0167-8809(00)00176-6.

McGroddy, M. E., Silver, W. L., Oliveira, R. C. de, Mello, W. Z. de, and Keller, M. (2008). Retention of phosphorus in highly weathered soils under a lowland Amazonian forest ecosystem. *Journal of Geophysical Research—Biogeosciences* 113. DOI: ArtnG0401210.1029/2008jg000756.

Mckenzie, R. H., Stewart, J. W. B., Dormaar, J. F., and Schaalje, G. B. (1992a). Long-term crop-rotation and fertilizer effects on phosphorus transformations .1. In a chernozemic Soil. *Can. J. Soil Sci.* 72, 569–579.

Mckenzie, R. H., Stewart, J. W. B., Dormaar, J. F., and Schaalje, G. B. (1992b). Long-term crop-rotation and fertilizer effects on phosphorus transformations .2. In a luvisolic Soil. *Can. J. Soil Sci.* 72, 581–589.

Meason, D. F., Idol, T. W., Friday, J. B., and Scowcroft, P. G. (2009). Effects of fertilisation on phosphorus pools in the volcanic soil of a managed tropical forest. *For. Ecol. Manage.* 258, 2199–2206. DOI: 10.1016/j.foreco.2009.04.001.

Menzies, N. W., Skilton, J. A., and Guppy, C. N. (1999). Phosphorus storage on effluent irrigated land. *J. Environ. Qual.* 28, 750–754.

Messiga, A. J., Ziadi, N., Plénet, D., Parent, L.-E., and Morel, C. (2010). Long-term changes in soil phosphorus status related to P budgets under maize monoculture and mineral P fertilization. *Soil Use and Management* 26.3, 354–364. DOI: 10.1111/j.1475-2743.2010.00287.x.

Messiga, A. J., Ziadi, N., Bélanger, G., and Morel, C. (2012). Process-based mass-balance modeling of soil phosphorus availability in a grassland fertilized with N and P. *Nutri. Cycl. Agroecosyst.* 92.3, 273–287. DOI: 10.1007/s10705-012-9489-x.

Messiga, A. J., Ziadi, N., Mollier, A., Parent, L.-E., Schneider, A., and Morel, C. (2015). Process-based mass-balance modeling of soil phosphorus availability: Testing different scenarios in a long-term maize monoculture. *Geoderma* 243-244, 41–49. DOI: 10.1016/j.geoderma.2014.12.009.

Miller, A. J., Schuur, E. A. G., and Chadwick, O. A. (2001). Redox control of phosphorus pools in Hawaiian montane forest soils. *Geoderma* 102, 219–237. DOI: 10.1016/S0016-7061(01)00016-7.

Mirabello, M. J., Yavitt, J. B., Garcia, M., Harms, K. E., Turner, B. L., and Wright, S. J. (2013). Soil phosphorus responses to chronic nutrient fertilisation and seasonal drought in a humid lowland forest, Panama. *Soil Res.* 51, 215–221. DOI: 10.1071/SR12188.

Morel, C. (2001). The effects of soil solution P and time on the transfer of P ions in soils from the IMPHOS European Network. In: *The effect of phosphate fertilizer management strategies on soil phosphorus status and crop yields in some European countries*, 103–102.

Morel, C., Cachot, C., Martinez, J., Peu, P., Elsass, F., Robert, M., and Fardeau, J. (2004). Évolution sur 12 ans de la solubilité, mobilité et lixiviation du phosphate dans un sol ayant massivement reçu du lisier. *Étude et Gestion des sols* 11.4.

Morel, C. and Hinsinger, P. (1999). Root-induced mmodification of the exchange of phosphate ion between soil solution and soil solid phase. *Plant Soil* 211.1, 103–110. DOI: 10.1023/a:1004485432261.

Morel, C., Tiessen, H., Moir, J. O., and Stewart, J. W. B. (1994). Phosphorus transformations and availability under cropping and fertilization assessed by isotopic exchange. *Soil Sci. Soc. Am. J.* 58.5, 1439–1445. DOI: 10.2136/sssaj1994.03615995005800050023x.

Morel, C., Tunney, H., Plénet, D., and Pellerin, S. (2000). Transfer of phosphate ions between soil and solution: Perspectives in soil testing. *J. Environ. Qual.* 29.1, 50–59. DOI: 10.2134/jeq2000.00472425002900010007x.

Mortala, N. A. (2013). *Comportamiento de las formas de fósforo en un Ultisol con diferentes manejos de implantación forestal.* Tech. rep., p. 116.

Neufeldt, H., Silva, J. E. da, Ayarza, M. A., and Zech, W. (2000). Land-use effects on phosphorus fractions in Cerrado oxisols. *Biol. Fertil. Soils* 31, 30–37. DOI: 10.1007/s003740050620.

Newbery, D. M., Alexander, I. J., and Rother, J. A. (1997). Phosphorus dynamics in a lowland African rain forest: The influence of ectomycorrhizal trees. *Ecol. Monogr.* 67, 367–409.

Nguyen, H., Schoenau, J. J., Van Rees, K., Nguyen, D., and Qian, R. (2001). Long-term nitrogen, phosphorus and potassium fertilization of cassava influences soil chemical properties in North Vietnam. *Can. J. Soil Sci.* 81, 481–488.

Nikonov, V. V. (1979). Characteristics of soil formation in the northern taiga spruce biogeocenoses of the Kola peninsula. *Soviet Soil Science* 11, 501–511.

Oberson, A., Fardeau, J. C., Besson, J. M., and Sticher, H. (1993a). Soil phosphorus dynamics in cropping systems managed according to conventional and biological agricultural methods. *Biol. Fertil. Soils* 16.2, 111–117. DOI: 10.1007/bf00369411.

Oberson, A., Fardeau, J. C., Besson, J. M., and Sticher, H. (1993b). Soil-Phosphorus Dynamics in Cropping Systems Managed According to Conventional and Biological Agricultural Methods. *Biol. Fertil. Soils* 16, 111–117. DOI: 10.1007/Bf00369411.

Oberson, A., Friesen, D., Tiessen, H., Morel, C., and Stahel, W. (1999). Phosphorus status and cycling in native savanna and improved pastures on an acid low-P Colombian Oxisol. *Nutri. Cycl. Agroecosyst.* 55.1, 77–88. DOI: 10.1023/a:1009813008445.

Oehl, F. (1999). Microbially mediated phosphorus transformation processes in cultivated soils. PhD thesis. ETH, Swiss Federal Institute of Technology.

Oehl, F., Frossard, E., Fliessbach, A., Dubois, D., and Oberson, A. (2004). Basal organic phosphorus mineralization in soils under different farming systems. *Soil Biol. Biochem.* 36.4, 667–675. DOI: 10.1016/j.soilbio.2003.12.010.

Ohalloran, I. P., Stewart, J. W. B., and Dejong, E. (1987). Changes in P-Forms and Availability as Influenced by Management-Practices. *Plant Soil* 100, 113–126. DOI: 10.1007/Bf02370935.

Otabbong, E., Persson, J., Iakimenko, O., and Sadovnikova, L. (1997). The Ultuna long-term soil organic matter experiment .2. Phosphorus status and distribution in soils. *Plant Soil* 195, 17–23. DOI: 10.1023/A:1004276732679.

Owusu-Bennoah, E. and Acquaye, D. K. (1996). Greenhouse evaluation of agronomic potential of different sources of phosphate fertilizer in a typical concretionary soil of northern Ghana. *Fertil. Res.* 44, 101–106.

Paniagua, A., Mazzarino, M. J., Kass, D., Szott, L., and Fernandez, C. (1995). Soil-Phosphorus Fractions under 5 Tropical Agroecosystems on a Volcanic Soil. *Aust. J. Soil Res.* 33, 311–320. DOI: 10.1071/Sr9950311.

Pare, D. and Bernier, B. (1989). Origin of the Phosphorus Deficiency Observed in Declining Sugar Maple Stands in the Quebec Appalachians. *Can. J. For. Res.* 19, 24–34. DOI: 10.1139/X89-004.

Patzold, S., Hejcman, M., Barej, J., and Schellberg, J. (2013). Soil phosphorus fractions after seven decades of fertilizer application in the Rengen Grassland Experiment. *J. Plant Nutr. Soil Sci.* 176, 910–920. DOI: 10.1002/jpln.201300152.

Pavinato, P. S., Merlin, A., and Rosolem, C. A. (2009). Phosphorus fractions in Brazilian Cerrado soils as affected by tillage. *Soil Tillage Res.* 105, 149–155. DOI: 10.1016/j.still.2009.07.001.

Perroni, Y., Garcia-Oliva, F., Tapia-Torres, Y., and Souza, V. (2014). Relationship between soil P fractions and microbial biomass in an oligotrophic grassland-desert scrub system. *Ecol. Res.* 29, 463–472. DOI: 10.1007/s11284-014-1138-1.

Pinochet, D., Epple, G., and MacDonald, R. (2001). Organic and inorganic phosphorus fractions in a soil transect of volcanic and metamorphic origin. *R.C. Suelo Nutr. Veg.* 1, 58–69.

Pizzeghello, D., Berti, A., Nardi, S., and Morari, F. (2011). Phosphorus forms and P-sorption properties in three alkaline soils after long-term mineral and manure applications in north-eastern Italy. *Agric. Ecosyst. Environ.* 141.1-2, 58–66. DOI: 10.1016/j.agee.2011.02.011.

Quesada, C. A., Lloyd, J., Schwarz, M., Patino, S., Baker, T. R., Czimczik, C., Fyllas, N. M., Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizao, F. J., Arneth, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. A., Geilmann, H., Moraes, J. O., Carvalho, F. P., Araujo, R. N., Chaves, J. E., Cruz, O. F., Pimentel, T. P., and Paiva, R. (2010). Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* 7, 1515–1541. DOI: 10.5194/bg-7-1515-2010.

Quintero, C. E., Gutierrez-Boem, F. H., Befani, M. R., and Boschetti, N. G. (2007). Effects of soil flooding on P transformations in soils of the Mesopotamia region, Argentina. *J. Plant Nutr. Soil Sci.* 170, 500–505. DOI: 10.1002/jpln.200625015.

Rabeharisoa, R. (2004). Gestion de la fertilité et de la fertilisation phosphatée des sols ferrallitiques des hautes terres de Madagascar. PhD thesis. Université d'Antanarivo.

Randriamanantsoa, L., Frossard, E., Oberson, A., and Bünemann, E. K. (2015). Gross organic phosphorus mineralization rates can be assessed in a Ferralsol using an isotopic dilution method. *Geoderma* 257-258, 86–93. DOI: 10.1016/j.geoderma.2015.01.003.

Randriamanantsoa, L., Morel, C., Rabeharisoa, L., Douzet, J.-M., Jansa, J., and Frossard, E. (2013). Can the isotopic exchange kinetic method be used in soils with a very low water

extractable phosphate content and a high sorbing capacity for phosphate ions? *Geoderma* 200-201, 120–129. DOI: 10.1016/j.geoderma.2013.01.019.

Reddy, D. D., Rao, S. A., and Singh, M. (2005). Changes in P fractions and sorption in an Alfisol following crop residues application. *J. Plant Nutr. Soil Sci.* 168, 241–247. DOI: 10.1002/jpln.200421444.

Reddy, K. S., Rao, A. S., and Takkar, P. N. (1996). Transformation of fertilizer P in a Vertisol amended with farmyard manure. *Biol. Fertil. Soils* 22, 279–282. DOI: 10.1007/s003740050111.

Redel, Y. D., Rubio, R., Rouanet, J. L., and Borie, F. (2007). Phosphorus bioavailability affected by tillage and crop rotation on a Chilean volcanic derived Ultisol. *Geoderma* 139, 388–396. DOI: 10.1016/j.geoderma.2007.02.018.

Redel, Y., Rubio, R., Godoy, R., and Borie, F. (2008). Phosphorus fractions and phosphatase activity in an Andisol under different forest ecosystems. *Geoderma* 145, 216–221. DOI: 10.1016/j.geoderma.2008.03.007.

Richter, D. D., Allen, H. L., Li, J. W., Markewitz, D., and Raikes, J. (2006). Bioavailability of slowly cycling soil phosphorus: major restructuring of soil P fractions over four decades in an aggrading forest. *Oecologia* 150, 259–271. DOI: 10.1007/s00442-006-0510-4.

Roberts, T. L., Stewart, J. W. B., and Bettany, J. R. (1985). The Influence of Topography on the Distribution of Organic and Inorganic Soil-Phosphorus across a Narrow Environmental Gradient. *Can. J. Soil Sci.* 65, 651–665.

Rose, T. J., Hardiputra, B., and Rengel, Z. (2010). Wheat, canola and grain legume access to soil phosphorus fractions differs in soils with contrasting phosphorus dynamics. *Plant Soil* 326, 159–170. DOI: 10.1007/s11104-009-9990-4.

Rubio, G., Faggioli, V., Scheiner, J. D., and Gutierrez-Boem, F. H. (2012). Rhizosphere phosphorus depletion by three crops differing in their phosphorus critical levels. *J. Plant Nutr. Soil Sci.* 175. DOI: 10.1002/jpln.201200307.

Ruckamp, D., Amelung, W., Theisz, N., Bandeira, A. G., and Martius, C. (2010). Phosphorus forms in Brazilian termite nests and soils: Relevance of feeding guild and ecosystems. *Geoderma* 155, 269–279. DOI: 10.1016/j.geoderma.2009.12.010.

Saa, A., Trasar-Cepeda, M. C., and Carballas, T. (1998). Soil P status and phosphomonoesterase activity of recently burnt and unburnt soil following laboratory incubation. *Soil Biol. Biochem.* 30, 419–428. DOI: 10.1016/S0038-0717(97)00120-X.

Salcedo, I. H., Bertino, F., and Sampaio, E. V. S. B. (1991). Reactivity of phosphorus in northeastern Brazilian soils assessed by isotopic dilution. *Soil Sci. Soc. Am. J.* 55.1, 140–145. DOI: 10.2136/sssaj1991.03615995005500010025x.

Saltali, K., Kilic, K., and Kocyigit, R. (2007). Changes in sequentially extracted phosphorus fractions in adjacent arable and grassland ecosystems. *Arid Land Research and Management* 21, 81–89. DOI: 10.1080/15324980601074602.

Sattell, R. R. and Morris, R. A. (1992). Phosphorus Fractions and Availability in Sri-Lankan Alfisols. *Soil Sci. Soc. Am. J.* 56, 1510–1515.

Satti, P., Mazzarino, M. J., Roselli, L., and Crego, P. (2007). Factors affecting soil P dynamics in temperate volcanic soils of southern Argentina. *Geoderma* 139, 229–240. DOI: 10.1016/j.geoderma.2007.02.005.

Scharer, M. (2003). The influence of processes controlling phosphorus availability on phosphorus losses in grassland soils. PhD thesis. ETH, Swiss Federal Institute of Technology.

Schoenau, J. J., Stewart, J. W. B., and Bettany, J. R. (1989). Forms and Cycling of Phosphorus in Prairie and Boreal Forest Soils. *Biogeochemistry* 8, 223–237.

Scott, D. A. and Bliss, C. M. (2012). Phosphorus Fertilizer Rate, Soil P Availability, and Long-Term Growth Response in a Loblolly Pine Plantation on a Weathered Ultisol. *Forests* 3, 1071–1085. DOI: 10.3390/f3041071.

Scott, J. T. and Condron, L. M. (2003). Dynamics and availability of phosphorus in the rhizosphere of a temperate silvopastoral system. *Biol. Fertil. Soils* 39, 65–73. DOI: 10.1007/s00374-003-0678-2.

Sharpley, A. N., Jones, C. A., Gray, C., Cole, C. V., Tiessen, H., and Holzhey, C. S. (1985). *A detailed phosphorus characterization of seventy-eight soils.* Tech. rep., p. 30.

Sharpley, A. N., McDowell, R. W., and Kleinman, P. J. A. (2004). Amounts, forms, and solubility of phosphorus in soils receiving manure. *Soil Sci. Soc. Am. J.* 68, 2048–2057.

Sheklabadi, M., Mahmoudzadeh, H., Mahboubi, A. A., Gharabaghi, B., and Ahrens, B. (2014). Land use effects on phosphorus sequestration in soil aggregates in western Iran. *Environ. Monit. Assess.* 186, 6493–6503. DOI: 10.1007/s10661-014-3869-4.

Shiels, A. B. and Sanford, R. L. (2001). Soil nutrient differences between two krummholz-form tree species and adjacent alpine tundra. *Geoderma* 102, 205–217. DOI: 10.1016/S0016-7061(01)00015-5.

Sinaj, S., Frossard, E., and Fardeau, J. C. (1997). Isotopically exchangeable phosphate in size fractionated and unfractionated soils. *Soil Sci. Soc. Am. J.* 61.5, 1413–1417. DOI: 10.2136/sssaj1997.03615995006100050019x.

Singh, M., Reddy, K. S., Singh, V. P., and Rupa, T. R. (2007). Phosphorus availability to rice (Oriza sativa L.)-wheat (Triticum estivum L.) in a Vertisol after eight years of inorganic and organic fertilizer additions. *Bioresour. Technol.* 98, 1474–1481. DOI: 10.1016/j.biortech.2006.02.045.

Slazak, A., Freese, D., Matos, E. D., and Huttl, R. F. (2010). Soil organic phosphorus fraction in pine-oak forest stands in Northeastern Germany. *Geoderma* 158, 156–162. DOI: 10.1016/j.geoderma.2010.04.023.

Soinne, H., Raty, M., and Hartikainen, H. (2010). Effect of air-drying on phosphorus fractions in clay soil. *J. Plant Nutr. Soil Sci.* 173, 332–336. DOI: 10.1002/jpln.200900225.

Solomon, D. and Lehmann, J. (2000). Loss of phosphorus from soil in semi-arid northern Tanzania as a result of cropping: evidence from sequential extraction and ^{31}P-NMR spectroscopy. *Eur. J. Soil Sci.* 51, 699–708.

Solomon, D., Lehmann, J., Mamo, T., Fritzsche, F., and Zech, W. (2002). Phosphorus forms and dynamics as influenced by land use changes in the sub-humid Ethiopian highlands. *Geoderma* 105, 21–48.

Spears, J. D. H., Lajtha, K., Caldwell, B. A., Pennington, S. B., and Vanderbilt, K. (2001). Species effects of Ceanothus velutinus versus Pseudotsuga menziesii, Douglas-fir, on soil phosphorus and nitrogen properties in the Oregon cascades. *For. Ecol. Manage.* 149, 205–216. DOI: 10.1016/S0378-1127(00)00555-7.

Spohn, M., Ermak, A., and Kuzyakov, Y. (2013). Microbial gross organic phosphorus mineralization can be stimulated by root exudates — A 33P isotopic dilution study. *Soil Biol. Biochem.* 65, 254–263. DOI: 10.1016/j.soilbio.2013.05.028.

Stroia, C., Morel, C., and Jouany, C. (2007). Dynamics of diffusive soil phosphorus in two grassland experiments determined both in field and laboratory conditions. *Agric. Ecosyst. Environ.* 119.1-2, 60–74. DOI: 10.1016/j.agee.2006.06.007.

Su, J., Wang, H., Kimberley, M. O., Beecroft, K., Magesan, G. N., and Hu, C. (2007). Fractionation and mobility of phosphorus in a sandy forest soil amended with biosolids. *Environ. Sci. Pollut. Res.* 14, 529–535. DOI: 10.1065/espr2007.08.443.

Suarez, E. R., Pelletier, D. M., Fahey, T. J., Groffman, P. M., Bohlen, P. J., and Fisk, M. C. (2003). Effects of exotic earthworms on soil phosphorus cycling in two broadleaf temperate forests. *Ecosystems* 7, 28–44. DOI: 10.1007/s10021-003-0128-x.

Sugihara, S., Funakawa, S., Nishigaki, T., Kilasara, M., and Kosaki, T. (2012). Dynamics of fractionated P and P budget in soil under different land management in two Tanzanian croplands with contrasting soil textures. *Agric. Ecosyst. Environ.* 162, 101–107. DOI: 10.1016/j.agee.2012.07.019.

Sugihara, S., Shibata, M., Mvondo Ze, A. D., Araki, S., and Funakawa, S. (2014). Effect of vegetation on soil C, N, P and other minerals in Oxisols at the forest-savanna transition zone of central Africa. *Soil Sci. Plant Nutr.* 60, 45–59. DOI: 10.1080/00380768.2013.866523.

Sui, Y. B., Thompson, M. L., and Shang, C. (1999). Fractionation of phosphorus in a mollisol amended with biosolids. *Soil Sci. Soc. Am. J.* 63, 1174–1180.

Sun, H. Y., Wu, Y. H., Yu, D., and Zhou, J. (2013). Altitudinal Gradient of Microbial Biomass Phosphorus and Its Relationship with Microbial Biomass Carbon, Nitrogen, and Rhizosphere Soil Phosphorus on the Eastern Slope of Gongga Mountain, SW China. *PLoS ONE* 8. DOI: ARTNe7295210.1371/journal.pone.0072952.

Svetlova, Y. I. and Gradusov, B. P. (1985). Mineral and chemical composition of soils from the southern taiga subzone of the Ural region. *Soviet Soil Science* 17, 97–102.

Takeda, M., Nakamoto, T., Miyazawa, K., and Murayama, T. (2009). Phosphorus transformation in a soybean-cropping system in Andosol: effects of winter cover cropping and compost application. *Nutri. Cycl. Agroecosyst.* 85, 287–297. DOI: 10.1007/s10705-009-9267-6.

Taranto, M. T., Adams, M. A., and Polglase, P. J. (2000). Sequential fractionation and characterisation (P-31-NMR) of phosphorus-amended soils in Banksia integrifolia (L.f.) woodland and adjacent pasture. *Soil Biol. Biochem.* 32, 169–177. DOI: 10.1016/S0038-0717(99)00138-8.

Tchienkoua and Zech, W. (2003). Chemical and spectral characterization of soil phosphorus under three land uses from an Andic Palehumult in West Cameroon. *Agric. Ecosyst. Environ.* 100, 193–200. DOI: 10.1016/S0167-8809(03)00195-6.

Thomas, S. M., Johnson, A. H., Frizano, J., Vann, D. R., Zarin, D. J., and Joshi, A. (1999). Phosphorus fractions in montane forest soils of the Cordillera de Piuchue, Chile: biogeochemical implications. *Plant Soil* 211, 139–148. DOI: 10.1023/A:1004686213319.

Tiessen, H., Abekoe, M. K., Salcedo, I. H., and Owusu-Bennoah, E. (1993). Reversibility of phosphorus sorption by ferruginous nodules. *Plant Soil* 153.1, 113–124. DOI: 10.1007/bf00010550.

Tiessen, H., Salcedo, I. H., and Sampaio, E. V. S. B. (1992). Nutrient and Soil Organic-Matter Dynamics under Shifting Cultivation in Semiarid Northeastern Brazil. *Agric. Ecosyst. Environ.* 38, 139–151. DOI: 10.1016/0167-8809(92)90139-3.

Tolchelnikov, Y. and Gurov, A. (1985). Seasonal dynamics of iron aluminum and silicon compounds in sandy soils of southern taiga in the european USSR. *Soviet Soil Science* 17, 32–48.

Townsend, A. R., Asner, G. P., Cleveland, C. C., Lefer, M. E., and Bustamante, M. M. C. (2002). Unexpected changes in soil phosphorus dynamics along pasture chronosequences in the humid tropics. *Journal of Geophysical Research—Atmospheres* 107. DOI: Artn806710.1029/2001jd000650.

Tran, T. S., Giroux, M., and Fardeau, J. C. (1988). Effects of soil properties on plant-available phosphorus determined by the Iiotopic dilution phosphorus-32 method. *Soil Sci. Soc. Am. J.* 52.5, 1383–1390. DOI: 10.2136/sssaj1988.03615995005200050033x.

Trasar-Cepeda, M. C., Gilsotres, F., and Guitianojea, F. (1990). Relation between Phosphorus Fractions and Development of Soils from Galicia (Nw Spain). *Geoderma* 47, 139–150. DOI: 10.1016/0016-7061(90)90051-A.

Turan, M., Ataoglu, N., and Sahin, F. (2007). Effects of Bacillus FS-3 on growth of tomato (Lycopersicon esculentum L.) plants and availability of phosphorus in soil. *Plant Soil and Environment* 53, 58–64.

Turrion, M. B., Glaser, B., Solomon, D., Ni, A., and Zech, W. (2000). Effects of deforestation on phosphorus pools in mountain soils of the Alay Range, Khyrgyzia. *Biol. Fertil. Soils* 31, 134–142. DOI: 10.1007/s003740050636.

Ubugunov, L. L., Ubugunova, V. I., and Mangataev, T. D. (1998). Phosphate reserves of the most typical alluvial soils of the Selenga river basin. *Eurasian Soil Sci.* 31, 61–66.

Valdespino, P., Romualdo, R., Cadenazzi, L., and Campo, J. (2009). Phosphorus cycling in primary and secondary seasonally dry tropical forests in Mexico. *Ann. For. Sci.* 66. DOI: Artn10710.1051/Forest:2008075.

Vaychis, M. V. (1988). Specific characteristics of Brown Forest soil formation on ancient alluvium. *Soviet Soil Science* 20, 50–56.

Verma, S., Subehia, S. K., and Sharma, S. P. (2005). Phosphorus fractions in an acid soil continuously fertilized with mineral and organic fertilizers. *Biol. Fertil. Soils* 41, 295–300. DOI: 10.1007/s00374-004-0810-y.

Vinegla, B., Garcia-Ruiz, R., Lietor, J., Ochoa, V., and Carreira, J. A. (2006). Soil phosphorus availability and transformation rates in relictic pinsapo fir forests from southern Spain. *Biogeochemistry* 78, 151–172. DOI: 10.1007/s10533-005-3698-1.

Vu, D. T., Tang, C., and Armstrong, R. D. (2008). Changes and availability of P fractions following 65 years of P application to a calcareous soil in a Mediterranean climate. *Plant Soil* 304, 21–33. DOI: 10.1007/s11104-007-9516-x.

Wagar, B. I., Stewart, J. W. B., and Moir, J. O. (1986). Changes with Time in the Form and Availability of Residual Fertilizer Phosphorus on Chernozemic Soils. *Can. J. Soil Sci.* 66, 105–119.

Wang, G. P., Liu, J. S., Wang, J. D., and Yu, J. B. (2006). Soil phosphorus forms and their variations in depressional and riparian freshwater wetlands (Sanjiang Plain, Northeast China). *Geoderma* 132, 59–74. DOI: 10.1016/j.geoderma.2005.04.021.

Wang, X., Lester, D. W., Guppy, C. N., Lockwood, P. V., and Tang, C. (2007). Changes in phosphorus fractions at various soil depths following long-term P fertiliser application on a black vertosol from south-eastern Queensland. *Aust. J. Soil Res.* 45, 524–532. DOI: 10.1071/SR07069.

Weiss, L., Shiels, A. B., and Walker, L. R. (2005). Soil impacts of bristlecone pine (Pinus longaeva) tree islands on alpine tundra, Charleston Peak, Nevada. *Western North American Naturalist* 65, 536–540.

Wright, R. B., Lockaby, B. G., and Walbridge, M. R. (2001). Phosphorus availability in an artificially flooded southeastern floodplain forest soil. *Soil Sci. Soc. Am. J.* 65, 1293–1302.

Xavier, F. A. D., Almeida, E. F., Cardoso, I. M., and Mendonca, E. D. (2011). Soil phosphorus distribution in sequentially extracted fractions in tropical coffee-agroecosystems in the Atlantic Forest biome, Southeastern Brazil. *Nutri. Cycl. Agroecosyst.* 89, 31–44. DOI: 10.1007/s10705-010-9373-5.

Xu, G., Sun, J. N., Xu, R. F., Lv, Y. C., Shao, H. B., Yan, K., Zhang, L. H., and Blackwell, M. S. A. (2011). Effects of air-drying and freezing on phosphorus fractions in soils with different organic matter contents. *Plant Soil and Environment* 57, 228–234.

Xue, Q. Y., Shamsi, I. H., Sun, D. S., Ostermann, A., Zhang, Q. C., Zhang, Y. S., and Lin, X. Y. (2013). Impact of manure application on forms and quantities of phosphorus in a Chinese Cambisol under different land use. *J. Soils Sediments* 13, 837–845. DOI: 10.1007/s11368-012-0627-5.

Yavitt, J. B., Harms, K. E., Garcia, M. N., Mirabello, M. J., and Wright, S. J. (2011). Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. *Austral Ecol.* 36, 433–445. DOI: 10.1111/j.1442-9993.2010.02157.x.

Zhang, J., Li, M., Liu, S., Liu, Y. J., Zhang, L. Q., Cao, Q., and Sun, D. Z. (2011a). Seasonal variations and bioavailability of inorganic phosphorus in soils of Yeyahu Wetland in Beijing, China. *Int. J. Sediment Res.* 26, 181–192.

Zhang, L., Wu, Y., Wu, N., Luo, P., Liu, L., and Hu, H. Y. (2011b). Impacts of Vegetation Type on Soil Phosphorus Availability and Fractions near the Alpine Timberline of the Tibetan Plateau. *Pol. J. Ecol.* 59, 307–316.

Zhang, Q., Wang, G. H., Feng, Y. K., Sun, Q. Z., Witt, C., and Dobermann, A. (2006). Changes in soil phosphorus fractions in a calcareous paddy soil under intensive rice cropping. *Plant Soil* 288, 141–154. DOI: 10.1007/s11104-006-9100-9.

Zhang, T. Q., MacKenzie, A. F., Liang, B. C., and Drury, C. F. (2004). Soil test phosphorus and phosphorus fractions with long-term phosphorus addition and depletion. *Soil Sci. Soc. Am. J.* 68, 519–528.

Zheng, Z. M., MacLeod, J. A., and Lafond, J. (2004). Phosphorus status of a Humic Cryaquept profile in a frigid continental climate as influenced by cropping practices. *Biol. Fertil. Soils* 39, 467–473. DOI: 10.1007/s00374-004-0735-5.

Zohar, I., Shaviv, A., Young, M., Kendall, C., Silva, S., and Paytan, A. (2010). Phosphorus dynamics in soils irrigated with reclaimed waste water or fresh water - A study using oxygen isotopic composition of phosphate. *Geoderma* 159, 109–121. DOI: 10.1016/j.geoderma.2010.07.002.

Zubillaga, M. S. and Giuffre, L. (1999). Soil phosphorus mobilization in different taxonomic orders. *J. Plant Nutr. Soil Sci.* 162, 201–205. DOI: 10.1002/(Sici)1522-2624(199903)162:2<201::Aid-Jpln201>3.0.Co;2-9.

Appendix E

Decomposition of ^{15}N-labelled litter and fate of nitrogen derived from litter in aspen forests and grasslands of south-western Siberia

Table E.1: Composition of the understorey vegetation in aspen forests (herbaceous, shrub and tree species with a height < 1.3 m and a diameter < 1 cm) and herbaceous vegetation in grasslands.

Site	n[a]	Dominant species[b]
Aspen forest		
BAR	14–18	*Populus tremula* L., *Heracleum sibiricum* L.
SAE	20–44	*Populus tremula* L., *Carex pallescens* L., *Phlomis tuberosa* L.
SAW	11–17	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth, *Betula pendula* Roth, *Urtica dioica* L.
TOM	16–29	*Populus tremula* L., *Athyrium filix-femina* (L.) Roth
Grassland		
BAR	13–17	*Bromopsis inermis* (Leys.) Holub, *Cuscuta europaea* L., *Festuca pseudovina* Hack. ex Wiesb.
SAE	22–60	*Bromopsis inermis* (Leys.) Holub, *Seseli ledebourii* G. Don fil., *Filipendula vulgaris* Moench
TOM	20–21	*Calamagrostis epigeios* (L.) Roth, *Bromopsis inermis* (Leys.) Holub, *Alopecurus pratensis* L.

[a]number of species over 3 plot replicates; [b]precisions in Chap. 5 (Brédoire et al. 2016)

Table E.2: Detailed characteristics of the forest and grassland study stands. (*n*) mean ± standard error of the mean.

Site	BAR	SAE	SAW	TOM
Forest				
Study area (m^2)	325	192	240	330
Trees[a] (*n*)	38	31	33	37
Aspen[ab] (%)	100	100	100	89
Density[a] ($n\,ha^{-1}$)	1169	1615	1375	1121
Basal area[a] ($m^2\,ha^{-1}$)	18.6	32.6	60.7	59.6
DBH[ac] (cm)	13.4 ± 0.8	15.4 ± 0.8	23.5 ± 0.6	25.1 ± 1.1
Height[ad] (m)	(24) 11 ± 0.5	(10) 15.9 ± 1.1	(13) 26.8 ± 0.7	(19) 21.5 ± 1.6
Age[ae] (years)	(5) 26 ± 3	(5) 37 ± 7	(5) 45 ± 2	(5) 74 ± 3
LAI[e]	4.94 ± 0.57	5.07 ± 0.59	5.03 ± 0.36	2.94 ± 0.46
Litterfall amount[f] ($g\,m^{-2}$)	(5) 363.96 ± 41.69	(4) 373.26 ± 43.52	(5) 370.52 ± 26.84	(5) 216.39 ± 33.55
$C_{litterfall}$[fg] ($g\,C\,kg^{-1}$)	(5) 455.06 ± 8.86	(4) 436.63 ± 27.14	(5) 396.08 ± 21.61	(5) 452.94 ± 19.59
$N_{litterfall}$[fg] ($g\,N\,kg^{-1}$)	(5) 13.58 ± 1.03	(4) 19.71 ± 1.72	(5) 18.87 ± 0.59	(5) 11.62 ± 0.37
Herbaceous[h] ($g\,m^{-2}$)	(3) 64.96 ± 1.87	(3) 78.31 ± 13.89	(3) 123.55 ± 21.97	(3) 79.2 ± 5.45
Grassland				
Herbaceous[h] ($g\,m^{-2}$)	(3) 213.87 ± 4.72	(3) 488.85 ± 36.39		(3) 298.98 ± 60.83

[a]values displayed for pole and tree stages (i.e. diameter at 1.30 m > 7 cm and height > 1.3 m);
[b]Other tree species: mostly *Betula pendula* but also, very rarely, *Abies sibirica*, *Padus avium*, *Pinus sibirica* and *Pinus sylvestris*; [c]DBH: diameter at breast height (1.30 m); [d]only aspen trees; [e]leaf area index; [f]collected in autumn 2013; [g]elemental concentration in litterfall; [h]aboveground green vegetation biomass (July 2013)

Table E.3: Isotopic composition of the soil layers sampled. Mean δ^{15}N (‰) and standard deviation of *n* samples.

	Nat.	Spring 2013			Spring 2014			Autumn 2014			Autumn 2015		
Soil layer	Ab	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd
BAR forest													
0–2.5 cm	2.53	3	3.88	0.40	3	8.36	4.74	3	6.50	1.11	3	7.79	0.67
2.5–5 cm	3.03	3	4.72	0.71	3	5.31	0.64	3	5.70	0.31	3	6.07	0.98
5–7.5 cm	3.74	3	5.37	0.92	3	6.98	0.55	3	5.87	0.47	3	5.29	0.29
7.5–10 cm	4.37	3	5.76	0.57	3	6.04	0.39	3	6.20	0.12	3	5.44	0.24
10–15 cm	4.61	3	6.06	0.58	3	6.92	1.19	3	6.24	0.09	3	5.99	0.07
SAE forest													
0–2.5 cm	3.29	3	3.89	0.37	3	4.49	1.03	3	8.03	1.65	3	5.69	1.37
2.5–5 cm	3.92	3	4.31	0.06	3	3.89	0.54	3	6.24	0.90	3	5.22	0.17
5–7.5 cm	4.62	2	5.00	0.26	3	2.22	1.97	3	6.05	0.44	3	5.78	0.12
7.5–10 cm	5.52	2	5.76	0.46	3	3.15	1.13	3	6.42	0.57	3	6.13	0.17
10–15 cm	5.59	2	6.95	0.80	3	3.00	1.33	3	6.40	0.39	3	6.32	0.04
SAW forest													
0–2.5 cm	2.56	3	5.37	1.81	3	14.74	10.17	3	15.52	1.44	3	8.52	1.53
2.5–5 cm	3.15	3	5.30	0.61	3	7.45	0.86	3	9.37	1.15	3	7.89	1.49
5–7.5 cm	4.06	3	5.38	0.49	3	6.46	0.47	3	6.32	0.54	3	6.46	0.34
7.5–10 cm	4.62	3	6.19	0.37	3	4.93	0.15	3	6.38	0.33	3	7.37	1.96
10–15 cm	4.70	3	7.74	1.57	3	5.76	2.02	3	6.32	0.15	3	6.88	0.78
TOM forest													
0–2.5 cm	3.12	3	8.82	1.64	3	11.35	1.00	3	15.81	1.41	3	11.67	0.89
2.5–5 cm	3.59	3	6.64	0.49	3	7.76	0.74	3	10.83	0.80	3	8.77	0.64
5–7.5 cm	3.53	3	7.88	2.58	3	6.53	0.34	3	8.05	0.22	3	7.68	0.66
7.5–10 cm	4.17	3	6.12	0.22	3	7.38	0.40	3	7.46	0.93	3	6.88	0.96
10–15 cm	5.04	3	6.53	0.76	3	7.41	0.42	3	7.20	0.76	3	6.73	0.41
BAR grassland													
0–2.5 cm	2.91	3	8.95	1.42	2	27.96	24.70	3	23.31	8.13	·	·	·
2.5–5 cm	4.19	3	7.34	0.15	1	5.28	NA	3	7.72	0.56	·	·	·
5–7.5 cm	4.86	3	7.31	0.29	1	2.26	NA	3	6.96	0.35	·	·	·
7.5–10 cm	5.06	3	6.93	0.04	1	0.77	NA	3	6.34	0.29	·	·	·
10–15 cm	4.35	3	6.57	0.12	1	-0.03	NA	3	6.42	0.15	·	·	·
SAE grassland													
0–2.5 cm	2.94	3	13.69	1.40	3	19.08	3.64	3	68.74	29.07	3	33.59	6.58
2.5–5 cm	6.67	3	7.39	0.21	3	9.73	0.83	3	17.94	5.45	3	11.11	2.00
5–7.5 cm	7.73	3	7.11	0.26	3	8.47	1.43	3	11.01	0.84	3	7.82	0.13
7.5–10 cm	8.02	3	7.30	0.23	2	8.50	2.12	3	8.15	0.36	3	6.99	0.16
10–15 cm	8.44	3	7.11	0.11	3	7.67	1.11	3	6.77	0.20	3	6.51	0.14
TOM grassland													
0–2.5 cm	4.25	3	39.64	8.56	3	44.72	26.52	3	55.33	14.45	·	·	·
2.5–5 cm	5.39	3	14.62	1.45	3	21.70	10.92	3	17.65	3.01	·	·	·
5–7.5 cm	6.27	3	9.67	0.81	3	15.56	5.90	3	11.38	1.74	·	·	·
7.5–10 cm	7.28	3	11.15	3.70	3	12.14	1.83	3	9.18	1.79	·	·	·
10–15 cm	8.22	3	9.10	1.27	3	9.80	1.54	3	8.05	0.73	·	·	·

Nat. Ab.: Natural abundance · : not available

Titre : Impacts du changement global sur les cycles biogéochimiques de l'eau et des nutriments dans le système sol–plante et conséquences pour la croissance de la végétation en Sibérie du sud-ouest

Résumé : Dans un contexte de changement global, prédire l'évolution de la productivité de la végétation dans le sud-ouest (SO) Sibérien reste un défi du fait d'incertitudes fortes sur les processus régulant la disponibilité en eau et en nutriments. Nous avons mis en évidence des relations entre cycles biogéochimiques, climat et propriétés du sol sur six sites contrastés.

La croissance radiale des tiges de peuplier est principalement sensible au bilan hydrique du sol en forêt de steppe, au sud du SO Sibérien, alors qu'elle est stimulée par de hautes températures estivales en sub-taïga, dans le nord de la région.

Des mesures de terrain et des simulations du bilan hydrique du sol ont montré que la fonte des neiges est importante pour la recharge des réserves hydriques du sol au sud. Au nord, ces réserves sont souvent rechargées en automne. La fonte des neiges est alors associée à du drainage. De plus, au nord, une épaisse couverture de neige protège le sol du gel en hiver. La distribution des racines fines est plus profonde en forêt de steppe qu'en sub-taïga, impactée par le déficit hydrique et le gel.

L'homogénéité du statut en phosphore (P) des sols dans le SO Sibérien montre qu'il n'est pas encore très impacté par la pédogénèse. Les stocks en P élevés, notamment les formes disponibles pour les plantes, suggèrent que le P n'est pas et ne sera pas limitant dans le futur.

La décomposition des litières aériennes et la libération de l'azote (N) sont plus rapides en sub-taïga qu'en forêt de steppe. Un fort drainage pourrait expliquer un transfert profond du N dans les sols en sub-taïga. Cependant ces sols semblent efficaces pour retenir le N, limitant les pertes pour le système sol–plante.

Mots-Clés : Sibérie du sud-ouest, changement global, neige, température du sol, bilan hydrique du sol, cerne, phosphore, azote, racines fines, isotopes, peuplier, prairie

---

Title: Impacts of Global Change on the Biogeochemical Cycling of Water and Nutrients in the Soil–Plant System and Consequences for Vegetation Growth in South-Western Siberia

Abstract: Predicting the evolution of vegetation productivity in SW Siberia in the context of global change remains a challenge because of major uncertainties concerning the biogeochemical cycling and the plant-availability of water and nutrients. We provided insights on their relation to climate and soil properties, investigating six contrasting sites.

Aspen stem radial growth is mainly sensitive to soil water budget in the forest-steppe zone established in the south of SW Siberia while it is enhanced by high summer temperatures in the sub-taiga, in the north of the region.

Field measurements and water budget simulations revealed that snow-melt is important re-filling soil water reserves in the south. In the north, these reserves are mostly re-filled in autumn and snow-melt is associated with drainage. A thick snow-pack also prevents soil from freezing in winter in the sub-taiga. Water deficit and soil freezing largely impact the distribution of fine roots within the soil profile which is deeper in forest-steppe than in sub-taiga.

The homogeneous soil phosphorus (P) status in the region investigated revealed this nutrient has not been yet very impacted by contrasting soil processes. High P stocks, and in particular plant-available forms, suggest P is unlikely to be limiting under current and future conditions.

By contrast, we found differences in nitrogen (N) status. Above-ground litter decay and the release of N occurs faster in sub-taiga than in forest-steppe. Higher drainage may explain deeper N transfer in sub-taiga soils. However, sub-taiga soils also seem to be efficient in retaining N, limiting losses from the soil–plant system.

Keywords: south-western Siberia, global change, snow, soil temperature, soil water budget, tree-ring, phosphorus, nitrogen, fine roots, isotopes, aspen, grassland

---

Unité de recherche
Institut National de la Recherche Agronomique – Bordeaux Sciences Agro
UMR 1391 Interactions Sol Plante Atmosphère
71 Avenue Édouard Bourlaux, 33140 Villenave d'Ornon, France